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Establishment and management of planted birch

Prospects and challenges for sustainable forest management

Andis Zvirgzdins

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SWEDISH UNIVERSITY
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Cover: The collage illustrates the four thematic areas addressed in this thesis: spacing, browsing, thinning, and modelling of birch. Photos were taken at experimental sites in Sweden, Finland, and Latvia. All photographs were taken by Andis Zvirgzdins, except the photographs of the spacing trial (first row – first photo & third row – first photo), taken by Karl-Gösta Hedberg, and the moose photograph (third row – second photo), provided by Laura Juvany Canovas. The schematic illustrations, with the exception of the last image in the middle row, were AI-generated.

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Establishment and management of planted birch

Abstract

Silver birch (*Betula pendula* Roth) has traditionally played a secondary role in Swedish forestry, dominated by coniferous species such as Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.). However, the increasing need for more diversified and climate-resilient forestry, combined with the availability of genetically improved planting material through breeding programmes, has renewed interest in birch as a viable alternative. This thesis investigated key aspects of establishing and managing planted silver birch, with a particular focus on spacing, browsing by cervids, thinning strategies, and modelling growth of genetically improved material. The research questions were explored through short-term field trials, long-term experiments, and surveys in Sweden and Latvia, complemented by interviews with private forest owners in Sweden. Establishment-related results showed that diameter growth increases with wider spacing. Yet, higher initial density may also serve as a tool to manage the local browsing risk. Light-to-moderate browsing did not significantly reduce survival or height growth of silver birch, indicating on species' ability to compensate for early-stage browsing. However, the negative impact of browsing on tree quality suggests that protective measures depending on browsing risk are required. Management-related results demonstrated that heavy thinning resulted in the strongest individual tree diameter growth, albeit at the cost of total stand volume production. Furthermore, simulations of basal area development under varying levels of genetic gain revealed that improved material can substantially enhance stand productivity and reduce rotation length of planted silver birch stands. Overall, this thesis demonstrated that silver birch can be a viable alternative in Swedish forestry, offering high growth potential and resilience to browsing when properly managed. Thinning can further increase stand value by promoting high-quality timber, provided this aligns with the management goals.

Keywords: silver birch, plantations, establishment, browsing, cervids, management, diameter growth, volume production, modelling, genetically improved material

Etablering och skötsel av planterade björkbestånd

Sammanfattning

Vårtbjörk (*Betula pendula* Roth) har traditionellt spelat en mindre roll i svenskt skogsbruk som har dominerats av gran (*Picea abies* L.) och tall (*Pinus sylvestris* L.). Dock har behovet av en ökad diversitet av trädslag för en mer klimatanpassad skogsskötsel, kombinerat med tillgången till genetiskt förädlade plantor bidragit till ett ökat intresse för björk. Denna avhandling undersöker viktiga skötselfrågor för föryngring och skötsel av vårtbjörk som val av planteringsförband, bete av hjortdjur, gallringsstrategier och tillväxtmodeller för genetiskt förädlat planteringsmaterial. Forskningsfrågorna studerades med en kombination av kort- och långsiktiga fältförsök, surveystudier och intervjuer med privata skogsägare. Resultaten visade att glesa förband vid plantering ökade diametertillväxten för enskilda träd men täta förband kan användas som ett sätt att kompensera för betesskador. Lätta till måttliga betesskador medförde ingen effekt på överlevnad eller höjdtillväxt hos planterade björkplantor vilket visar på björkens förmåga till kompensatorisk tillväxt. Resultaten visade dock på möjliga negativa effekter på framtida virkeskvalitet vilket kan motivera olika skydd mot bete beroende på betestryck. Gallringsstudierna visade att hårda gallringar resulterade i ökad diametertillväxt för enskilda träd men hårda gallringar minskade den totala volymproduktionen per hektar. Simuleringar av grundyteutveckling för plantmaterial med olika nivå av genetisk förädling visade att användning av förädlat plantmaterial kan öka produktionen och minska omloppstidens längd. Denna avhandling visar att vårtbjörk kan vara ett möjligt alternativ för svenskt skogsbruk med potential till hög produktion och relativt hög motståndskraft mot bete när den sköts på rätt sätt. Gallringsprogram med relativt hårda gallringar bidrar till snabb produktion av grovt virke av hög kvalitet ifall det är målet med skogsproduktionen.

Nyckelord: vårtbjörk, planteringar, etablering, viltbete, hjortdjur, skötsel, diameter-tillväxt, volymproduktion, modellering, genetiskt förbättrat material

Stādītu bērzu audžu ieaudzēšana un apsaimniekošana

Abstrakts

Kārpainais bērzs (*Betula pendula* Roth) tradicionāli Zviedrijas mežsaimniecībā ir ieņēmis sekundāru lomu, starp dominējošajām skuju koku sugām – parasto egli (*Picea abies* L.) un parasto priedi (*Pinus sylvestris* L.). Tomēr pieaugošā nepieciešamība pēc daudzveidīgākas un klimata izturīgākas mežsaimniecības, kā arī ģenētiski uzlabota stādu materiāla pieejamība selekcijas programmās, ir atjaunojusi interesi par bērzu. Šajā darbā tika pētīti galvenie kārpainā bērza stādīšanas un apsaimniekošanas aspekti, galveno uzmanību pievēršot: audžu biezībai, pārnadžu bojājumiem, krājas kopšanas stratēģijām un ģenētiski uzlabotā materiāla augšanas modelēšanai. Zinātniskie jautājumi tika pētīti, apvienojot lauka izmēģinājumus Zviedrijā un Latvijā, kā arī intervijas ar privātajiem meža īpašniekiem, kas tika īstenotas Zviedrijā. Rezultāti atklāja, ka koku diametra pieaugums palielinās, palielinot stādīšanas attālumu. Tomēr augstāks sākotnējais blīvums var būt efektīvs rīks pārnadžu risku pārvaldībā. Viegli līdz mēreni dzīvnieku bojājumi būtiski neietekmēja kārpainā bērza izdzīvotspēju vai augstumu, kas norāda uz sugas spēju kompensēt bojājumus agrīnajā stadijā. Taču bojājumu negatīvā ietekme uz koka kvalitāti liecina, ka nepieciešami aizsardzības pasākumi, atkarībā no pārnadžu populācijas līmeņa. Darba otrā daļa apliecināja, ka intensīva krājas kopšana veicina individuālo koka diametra pieaugumu, bet samazina kopējo krāju. Savukārt audzes šķērslaukuma simulācijas, pieņemot dažādus ģenētiskā ieguvuma līmeņus, atklāja: uzlabotais materiāls būtiski palielina audzes produktivitāti un saīsina rotācijas ilgumu. Kopumā darbs pierāda, ka, pareizi apsaimniekojot, kārpainais bērzs var būt konkurētspējīga alternatīva Zviedrijas mežsaimniecībā – ar augstu augšanas potenciālu un izturību pret pārnadažu bojājumiem. Savukārt krājas kopšana var veicināt augstas kvalitātes koksnes audzi un palielināt audzes vērtību, ja tas atbilst apsaimniekošanas mērķiem.

Atslēgas vārdi: kārpainais bērzs, bērzu plantācijas, meža ieaudzēšana, pārnadžu bojājumi, briežveidīgie, meža apsaimniekošana, diametra augšanas gaita, krājas tilpuma pieagumus, augšanas gaitas modelēšana, ģēnētiski selekcionēts materiāls

Preface

"He who thinks great thoughts, often makes great errors" – **Martin Heidegger**

Dedication

To my family

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. Zvirgzdins, Andis*; Romans, Edvards; Lula, Mikolaj; Hjelm, Karin; Nilsson, Urban (2025) Spacing matters: A case study of diameter development and volume production of silver birch and downy birch on former agricultural land in central Sweden. (manuscript)

II. Zvirgzdins, Andis*; Hjelm, Karin; Nilsson, Urban (2025). Understanding the impact of browsing by cervids on planted silver birch: perspectives from private forest owners and regional monitoring in Sweden. (manuscript)

III. Zvirgzdins, Andis*; Hjelm, Karin; Lula, Mikolaj; Liziniewicz, Mateusz; Nilsson, Urban (2025). Effect of simulated browsing on growth of silver birch. Scandinavian Journal of Forest Research, 1–17. https://doi.org/10.1080/02827581.2025.2537447

IV. Zvirgzdins, Andis*; Dosumu, Ola; Holmström, Emma; Liziniewicz, Mateusz; Fahlvik, Nils; Liepins, Kaspars; Romans, Edzus; Saicane, Dagnija; Nilsson, Urban (2025). Individual tree and stand growth of silver birch in the short and long term after thinning. (manuscript)

V. Liziniewicz, Mateusz; Barbeito, Ignacio; Zvirgzdins, Andis*; Stener, Lars-Goran; Niemisto, Pentti; Fahlvik, Nils; Johansson, Ulf; Karlsson, Bo; Nilsson, Urban (2022). Production of genetically improved silver birch plantations in southern and central Sweden.

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The contribution of Andis Zvirgzdins to the papers included in this thesis was as follows:

I. AZ is the main author. AZ and ER compiled the data. AZ did the statistical analysis and wrote the manuscript in collaboration with the co-authors.

II. AZ is the main author. AZ developed the research idea together with UN and KH. AZ managed the field trials. AZ compiled the data and did the statistical analysis. AZ wrote the manuscript in collaboration with the co-authors.

III. AZ is the main author. AZ developed the research idea together with UN, KH and ML. AZ established and managed the field trial. AZ compiled the data and did the statistical analysis. AZ wrote the manuscript in collaboration with the co-authors.

IV. AZ is the main author. AZ together with ER, DS, OD and ML managed the field trials. AZ together with OD and ML compiled the data. AZ and OD did the statistical analysis and wrote the manuscript in collaboration with the co-authors.

V. AZ participated in the data analysis (validation of the models) and writing of the manuscript which was led by ML

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Abbreviations

DBH	Diameter at breast height
GADA	Generalised algebraic difference approach
GLM	Generalised linear model
GLMM	Generalised linear mixed effects model
H	Tree height
LM	Linear model
LMM	Linear mixed effects model
m^{-3}sk ha^{-1} $year^{-1}$	Cubic metres of stem volume per ha per year, including bark
MAI	Mean annual increment
QMD	Quadratic mean diameter
RBD	Randomised block design
SI	Site index (measure of site productivity)
SIH	Site index derived from height growth of dominant trees (expressed in m at a specified reference age)

1. Introduction

The genus *Betula* L. comprises a group of broadleaf, deciduous tree species widely distributed across the temperate and boreal regions of the Northern Hemisphere (Ashburner & Mcallister 2016; Beck *et al.* 2016; Ireland & Ruxton 2022). With over 50 species recognised globally (Atkinson 1992; Ashburner & Mcallister 2016), birch trees are an ecologically significant components of many forest ecosystems, also holding considerable social and economic value in many regions. The widespread discernibility of birch trees is largely due to their distinctive white, paper-like bark, which is a present characteristic of most, but not all, species within the genus *Betula*. The visually appealing bark contains betulin (Demets et al. 2022), and owing to its physical and chemical properties, serves several important functions, like reflection of solar radiation (Henrion & Tributsch 2009), potentially protecting trees from excessive heat (Lev-Yadun 2019) and sunscald (Ireland & Ruxton 2022), as well as defending against herbivores by serving as a signal for bark-stripping mammals (Ireland & Ruxton 2022).

Across Europe, with a particularly notable presence in Northern Europe, the two most common and economically important naturally occurring species are silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.) (Niemistö *et al.* 2008; Hynynen *et al.* 2010; Beck *et al.* 2016). In Sweden, these species together account for approximately 12% of the total standing timber volume (Lidman *et al.* 2024b), complementing the Swedish forest landscape otherwise dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Skogsdata 2024).

In natural settings, silver birch and downy birch are seldom distinguished as both species have similar light canopies, serrated leaves and white paper-like bark (Hynynen *et al.* 2010; Beck *et al.* 2016), interspersed with dark-grey markings called lenticels (Fletcher *et al.* 2018). Both species are among the largest birch species when mature, reaching 25 – 35 m in height. However, more detailed inspection of the bark characteristics, leaves and shoots may help to distinguish between them (Hynynen *et al.* 2010). Silver and downy birch have the same monoecious reproductive system as other *Betula* species, with separate female and male catkins developing on the same tree (Niemistö *et al.* 2008; Ranta *et al.* 2008; Beck *et al.* 2016). Hybridisation between the two species seldom occurs due to differences in ploidy levels – silver birch is diploid (2n = 28) and downy birch is tetraploid (2n = 56) – which creates a genetic incompatibility (Hynynen *et al.* 2010). However, while ploidy level presents a significant obstacle, it is not an absolute barrier to hybridisation (Zohren *et al.* 2016).

Despite their widespread natural distribution, silver birch and downy birch have traditionally been undervalued in forestry, and their significance as timber species in Europe has varied over time. Although birch has become the most abundant commercial hardwood species in Northern Europe and the Baltic Sea region (Dubois *et al.* 2020), it remains secondary to conifers in terms of timber production in Sweden (Skogsstyrelsen 2020; KSLA 2024). However, both the value of birch wood and the interest in birch as a species have increased considerably in Sweden (Lidman *et al.* 2024b; Garfield & Brukas 2025), driven partly by enhanced growth of improved planting material, but also by the growing recognition of the importance of diversified forest stands and adaptive management strategies (Bakx *et al.* 2024; Felton *et al.* 2024; Lee *et al.* 2024).

1.1 Ecology of silver birch and downy birch

1.1.1 Ecological functions: reproduction, distribution and site preferences

Following the retreat of the ice sheets at the end of the Last Glacial Maximum, approximately 12,000 – 14,000 years ago, silver birch and downy birch were among the first tree species to re-colonise Sweden, closely followed by Scots pine, European aspen (*Populus tremula* L.) and mountain ash (*Sorbus aucuparia* L.) (Huntley & Birks 1983). These species formed a sparse tundra forest. After the arrival and continued progression of Norway spruce, the millennia-long dominance of birch slowly faded away. However, birch was always among the first species to re-occupy disturbed sites. The ability of *Betula spp.,* in general, to rapidly claim sites after natural disturbances like wind throws (Jonášová *et al.* 2010; Vodde *et al.* 2010; Bāders *et al.* 2021; Anoszko *et al.* 2022; Kellomäki 2022), wildfires (Niemistö *et al.* 2008; Ascoli & Bovio 2010; Laiviņš *et al.* 2019; Anoszko *et al.* 2022; Kellomäki 2022; Liu *et al.* 2022) and human disturbances, e.g., clearcutting of forest stands (Karlsson 2002; Götmark *et al.* 2005; Karlsson & Nilsson 2005; Niemistö *et al.* 2008; Kellomäki 2022) has remained a defining feature throughout its history in the Northern Hemisphere. Therefore, silver birch and downy birch are often characterised as species with broad ecological amplitudes, and both are recognised as pioneer species.

The ability of birches to colonise disturbed and open sites is largely due to their prolific seed production, effective seed dispersal strategies, and rapid initial growth (Fischer *et al.* 2002; Niemistö *et al.* 2008; Hynynen *et al.* 2010; Beck *et al.* 2016). Birch trees are wind-pollinated and their light seeds, also known as samaras, are in fact winged achenes. For silver birch, they are hairless with broad wings typically three times the width of the seed itself. In comparison, the samaras of downy birch are covered with fine hairs, and their wings are relatively narrow – approximately 1.5 times the seed's width (Niemistö *et al.* 2008). Both silver and downy birch can produce pollen and seeds in large quantities; however the production can vary greatly over successive years (Marquis 1969; Hjelmroos 1991; Wagner *et al.* 2004; Niemistö *et al.* 2008; Dreimanis 2016; Rousi *et al.* 2019). In Northern Europe, birch populations are typically capable of producing sufficient seed crops every 2 – 3 years (Hynynen *et al.* 2010), although it can be less frequent in northern locations (Niemistö *et al.* 2008). The variation in birch seed production may depend on individual tree size, which is best characterised by leaf mass or basal area (Holmström *et al.* 2017), but it can also vary depending on climate in conjunction with the interannual dynamics of resource allocation in trees (Ranta *et al.* 2005). Unfavourable weather conditions during pollination may also play a role, like rain, strong wind or even frost (Marquis 1969). Unsatisfactory pollination and consequently lower seed viability may also result from heightened stress conditions, such as weakened seed trees and diminished stem carbohydrate reserves (Evans 1988). However, in favourable conditions, birch seeds can be effectively dispersed over relatively large areas by wind. While most seeds typically disperse no more than 100 metres from the parent tree, in case of irregular terrain, e.g., slopes (Tiebel *et al.* 2020) or very strong winds (Liepiņa 2005), birch seeds may travel longer distances.

In Northern Europe, silver and downy birch frequently coexist, often occupying similar sites of varying soil conditions across a range of forest ecosystems (Niemistö *et al.* 2008; Dreimanis 2016). Despite this overlap, the two species exhibit distinct site preferences, allowing them to thrive under different environmental conditions (Perala & Alm 1990; Saramäki & Hytönen 2004; Hytönen *et al.* 2014; Beck *et al.* 2016). Silver birch prefers fertile sites, including abandoned agricultural lands (Koivisto 1959; Oikarinen 1983; Niemistö *et al.* 2008; Liepiņš *et al.* 2013). In terms of soil, silver birch exhibits a preference for well-drained sandy loam, fine sandy and silty till soils (Atkinson 1992; Niemistö *et al.* 2008; Hytönen *et al.* 2014; Lidman *et al.* 2024b). It does not tolerate compacted pure clay, silt soils, or waterlogged sites. Downy birch is a less-demanding species as it can tolerate a larger variety of substrates, including poor fertility, dry, and even stony sites. It is known to tolerate soils that are cool, fine textured and poorly aerated, including challenging environments like wet peatlands (Sutinen *et al.* 2002; Saramäki & Hytönen 2004; Niemistö *et al.* 2008; Hynynen *et al.* 2010; Hytönen *et al.* 2014; Lidman *et al.* 2024b). In Sweden, both species are naturally found throughout the country, except in mountain and near-mountain forests. Naturally occurring downy birch is relatively more common in the northern parts of the country and accounts for the largest proportion of total volume of birch nationwide (Rytter 2014; Fahlvik *et al.* 2021).

1.1.2 Growth characteristics and wood properties

The growth dynamics of birch are shaped by a range of ecological, environmental and management-related factors, including species choice, type of establishment, soil and site conditions, as well as climate and management practices applied.

As is typical of broadleaved tree species, birch exhibits a sympodial growth form (Niemistö *et al.* 2008; Hynynen *et al.* 2010; Lintunen *et al.* 2011; Tenkanen *et al.* 2020), with the leading shoot ceasing to grow and the lateral shoot overtaking the leader. Despite this growth habit, birch commonly displays a straight and slender stem (Heräjärvi 2001; Niemistö *et al.* 2008). Silver birch stems are generally straighter compared to downy birch (Verkasalo 1997). Being diffuse-porous hardwoods, the wood of birch is relatively uniform, with vessels evenly arranged across the growth rings (Dubois *et al.* 2020; Jones *et al.* 2023b), and with growth ring transitions that are subtle and often difficult to distinguish (Vanhellemont *et al.* 2016; Harr *et al.* 2021). Birch physical and mechanical properties, such as density, stiffness, strength, and hardness, are similar to beech (Dubois *et al.* 2020). The two birch species' wood properties differ minimally, with silver birch exhibiting a slight advantage over downy birch due to its relatively higher wood density (Heräjärvi 2004; Dubois *et al.* 2020; Jones *et al.* 2023b) when comparing trees of similar size. However, downy birch has been found to have straighter fibres than silver birch, a property improving dimensional stability of the wood (Jones *et al.* 2023a). In industrial application, no distinction is generally made between the two species (Heiskanen 1957; Luostarinen & Verkasalo 2000; Hytönen *et al.* 2014; Dreimanis 2016). Wood density appears to be negatively correlated with growth rate (Jones *et al.* 2023b). However, this relationship may not always be consistent, and is generally regarded as a small concession relative to the benefits of increased growth (Dunham *et al.* 1999).

During the juvenile stage, height growth of birch is rapid, with the fastest growth beginning when trees are around three to six metres tall. Height growth in naturally regenerated birch follows a more moderate trajectory compared to that of planted stands. In the first five growing seasons, planted birch can be up to three times taller than naturally regenerated birch

(Niemistö *et al.* 2008). Under optimal conditions, birch height growth can exceed one metre per year (Niemistö *et al.* 2008; Liepiņš *et al.* 2013). Silver birch can reach 24 – 25 metres in 30 years (Oikarinen 1983; Eriksson *et al.* 1997; Niemistö *et al.* 2008). Height growth of birch normally peaks at around 10 – 20 years, thereafter it slows down slightly, but vigorous growth continues until the age of 40 – 50 years (Oikarinen 1983).

Diameter growth, like height growth, begins rapidly and peaks before the age of 20 years. Unlike height growth, however, it is more sensitive to stand density and management interventions such as thinning (Niemistö *et al.* 2008; Hynynen *et al.* 2010). On well-suited sites, birch can exhibit annual diameter increments of 3 – 4 mm (Hynynen *et al.* 2010). However, in well-managed plantations on former agricultural sites, silver birch diameter can grow substantially faster, particularly during the early development phase (Liepiņš *et al.* 2013). Compared to naturally regenerated stands, planted birch diameter growth often peaks at a later stage (Oikarinen 1983; Niemistö *et al.* 2008). Furthermore, silver birch generally maintains a longer period of vigorous diameter growth compared to downy birch (Niemistö *et al.* 2008), likely due to its higher growth potential, especially on fertile sites.

Silver birch is considered to be the more productive species out of the two in both natural and artificial settings (Koivisto 1959; Raulo 1981; Dahlberg *et al.* 2006; Hytönen *et al.* 2014). According to Dahlberg et al. (2006), mean annual increment (MAI) for birch in Sweden ranges from 6 – 10 m^{-3}sk ha^{-1} year^{-1} with downy birch typically yielding 6 – 7 m^{3}sk ha^{-1} year^{-1} and silver birch up to 10 m^{3}sk ha^{-1} year^{-1} over a rotation period of 30 – 60 years. Both overall productivity and the differences observed between the two birch species may be shaped by site factors and the prevailing growth conditions (Karlsson *et al.* 1997; Liepiņš *et al.* 2013; Hytönen *et al.* 2014). In Latvia, growth rates for planted silver birch have been reported to range from 4 to 10 m^{3}sk ha year^{-1} depending on soil characteristics (Liepiņš *et al*. 2013). The lowest growth rates are observed on waterlogged and heavy clay soils, with an MAI of 3.8 – 5.5 m^{-3}sk ha^{-1} year^{-1} and rotation lengths of 35 and 45, years respectively. In contrast, the highest growth has been identified on podzol and calcaric cambisol soil types, with MAIs of 7.3 and 8.8 m^{-3}sk ha^{-1} year^{-1} at rotation lengths of 50 and 60 years, respectively. On former agricultural lands, planted silver birch has shown an MAI of up to 10 m^{-3}sk ha^{-1} $year^{-1}$ by age 15 (Liepiņš *et al.* 2013) at ordinary initial spacing configurations.

1.2 Genetic improvement and breeding programmes for birch

As forestry faces increasing production demands, tree breeding has increasingly been recognised as a sustainable and environmentally responsible approach to meet this goal (Pâques 2013; Rosvall & Mullin 2013; Jansson *et al.* 2017; Zeltiņš *et al.* 2024). Traditionally, breeding efforts have been directed toward the most commercially valuable species. Among other objectives, these efforts have focused on improving traits of economic importance (Pâques 2013; Ruotsalainen 2014; Stener 2015; Jansson *et al.* 2017), notably volume production, and to a lesser degree wood quality and resistance to environmental stresses. This emphasis on economically valuable traits has also guided species selection within broadleaves. Birch breeding programmes have primarily focused on silver birch, whose generally superior growth and wood quality have made it the preferred target of improvement efforts across Northern Europe (Viherä-Aarnio 1994; Jansson *et al.* 2017; Gailis *et al.* 2020b; Fahlvik *et al.* 2021; Jones *et al.* 2023a). However, certain programmes also conduct breeding in downy birch, although much less extensively (Jones *et al.* 2023a).

1.2.1 History and current status of birch breeding

Silver birch has historically received less breeding attention compared to the commercially dominant conifers. The first silver birch breeding programmes in Northern Europe began in the early 20th century, around the 1930s in Sweden and the 1940s in Finland. However, more coordinated work, including first crossing and progeny testing, took place in late 20th century, the 1960s in Finland (Johnsson 1974; Koski & Rousi 2005; Haapanen 2024), the 1980s in Sweden (Danell & Werner 1989b; Danell 1991; Stener & Jansson 2005), and the 1990s in Latvia and Estonia (Jansons 2008; Gailis *et al.* 2020b).

Similarly to other species, the silver birch improvement cycle began with the identification and selection of plus trees (Koski & Rousi 2005; Rosvall & Mullin 2013; Gailis *et al.* 2020b), i.e. individuals from both planted and natural stands that exhibit superior phenotypic traits such as height, diameter, stem form, and overall vitality. In Sweden, approximately 1300 silver birch plus trees were selected in the early 1990s. After genetic testing through progeny trials, a multiple-population breeding strategy was adopted – similar to the approach used for Norway spruce and Scots pine. Plus trees were tested via their progeny (half-sib families[1]) to provide breeding values, and seven populations of 50 trees each (three northern and four southern) were established to reflect regional adaptation (Fahlvik *et al.* 2021). Subsequent breeding has been conducted within these populations: controlled crossings are carried out, new progeny trials are planted, and selection forward is based on the results of these trials. In parallel, the establishment of both open-pollinated and greenhouse-based seed orchards has played a pivotal role in structuring silver birch breeding efforts and facilitating the large-scale production of improved reproductive material across national programmes (Jansons 2008; Fahlvik *et al.* 2021; Haapanen 2024), including Sweden's. As illustrated in the breeding cycle (Figure 1), this process is iterative and continuous, with each round of selection, testing, and evaluation feeding into the next generation to progressively enhance genetic gain and overall performance.

[1] Half-sib progenies are offspring sharing one known parent, typically, the mother parent tree, whereas full-sib family means that both the mother parent tree and father parent tree are known (White *et al.* 2007).

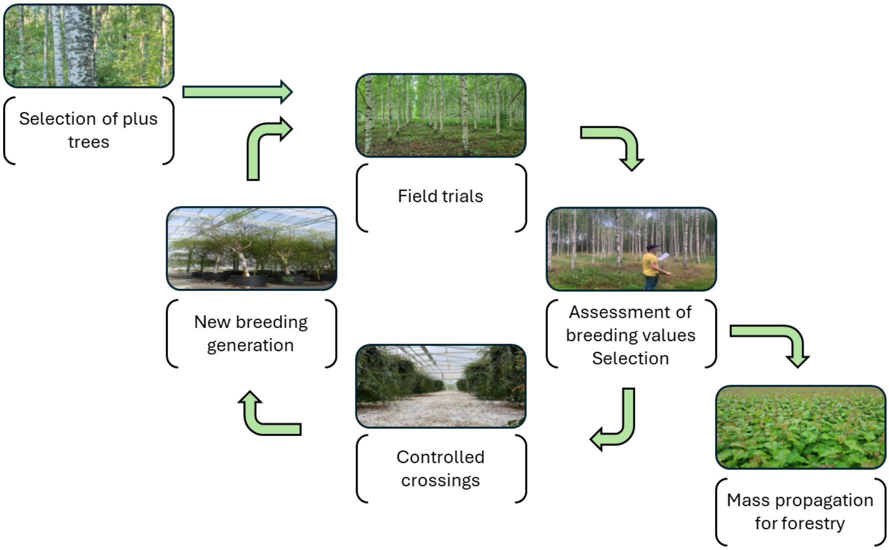

Figure 1. Tree initial breeding cycle for silver birch – the conventional breeding programme in Sweden. The cycle began with the selection of plus trees from natural stands (1990s), followed by the establishment of progeny trials and field tests. Superior individuals were identified through assessment of breeding values. The best-performing crosses among selected individuals formed the next breeding population. The improved material was then mass-propagated and used in operational forestry, while the breeding cycle resumed with the next generation of crossing, testing and selection. Subsequent cycles adhere to the same model, apart from the initial plus-tree selection. Photos: Andis Zvirgzdins.

Alongside traditional breeding, advanced molecular tools such as marker-assisted selection, and more notably genomic selection, have emerged as powerful complements to refine and speed up the breeding process (Grattapaglia 2017; Grattapaglia *et al.* 2018; Lebedev *et al.* 2020). In silver birch, the application of genomic selection is still relatively limited, especially when compared to species with sequenced genomes and more established genomic tools, like Norway spruce (Nystedt *et al.* 2013). However, the relatively compact genome of silver birch (Sharma *et al.* 2023), combined with favourable traits like early flowering (Salojärvi *et al.* 2017), makes it a promising candidate for advance genomic selection techniques.

1.2.2 The role of genetically improved material in forest management

The Swedish birch breeding programme emphasises vitality, productivity, and external wood quality as key selection traits (Stener & Jansson 2005; Fahlvik *et al.* 2021). The production of high-quality birch material is supported by both open-pollinated and greenhouse-based seed orchards. However, the greenhouse-based approach (Figure 2) has allowed for more targeted and impactful breeding efforts (Rosvall 2011), resulting in more precise and predictable genetic gain. Currently, the genetic gain in volume of bred birch material is expected to reach 5 – 20%, with open-pollinated progenies yielding gains of about 5 – 10% and progenies from greenhouse-based seed orchards reaching 15 – 20% (Rosvall *et al.* 2010; Haapanen *et al.* 2015), with considerable improvements in stem quality (Danell & Werner 1989a; Stener & Jansson 2005; Stener 2015; Jansson *et al.* 2017).

Genetic improvements from silver birch breeding have been shown to persist, with realised gains in stem volume and quality consistently observed across seed orchards, and stem volume gains even showing an increasing temporal trend (Haapanen 2024). This supports the notion that genetic gains could be maintained over time, contributing to increased production and reduced optimal rotation age (Rosvall 2011; Jansson *et al.* 2017). However, the advantages of enhanced growth and quality are often realised already during earlier stages of stand development. During the establishment phase, rapid early growth of bred planting material may help seedling reaching the necessary size to evade attacks from large herbivores faster. Enhanced growth can also improve economic outcomes throughout the rotation (Gailis *et al.* 2020a; Zeltiņš *et al.* 2025).

Figure 2. The “Ekebo 5 and 6” silver birch seed orchard in a greenhouse at Ekebo (Skogforsk). Ekebo 5 and 6 refer to the fifth or sixth set of clones used for seed-orchard establishment located in southern Sweden (south of 60°N), established to produce material adapted to this region. Photo: M. Liziniewicz.

1.3 The Swedish forest industry and birch's role in it

Sweden is a heavily forested country (Lindahl *et al.* 2017; Hertog *et al.* 2022), with forests covering around 70% of the total land area (KSLA 2024) or 27.9 million ha. Of this, around 84% is classified as productive forest land[2] (Skogsdata 2024). The forest sector is vital to Sweden, contributing significantly to the economy (Lundmark *et al.* 2013; Fischer *et al.* 2020) and supporting livelihoods in rural areas (KSLA 2024). When it comes to coniferous species, Sweden is among the ten largest producers of industrial roundwood (FAOSTAT 2023), and among the largest exporters of sawn wood, paper and paperboards (FAO 2024). In addition to their economic value, Sweden's forests are vital for climate change mitigation through carbon sequestration (Schulte *et al.* 2022; Felton *et al.* 2024; Laudon *et al.* 2024) and play a key ecological role in supporting biodiversity and ecosystem functioning (Gustafsson & Perhans 2010; Felton *et al.* 2016; Angelstam *et al.* 2020).

1.3.1 Market trends – historic and current industrial demand for birch wood and products

Historically, birch has held a complex and evolving role in Swedish forestry and society. In earlier times, birch was highly valued for its multifunctionality – providing firewood, bark for crafting and roofing (Liedgren & Östlund 2011), and potash for soap and glass production (Östlund *et al.* 1998). Before the rise of large-scale iron and timber exports in 17th century, birch bark, wood tar, and potash were among the region's most significant trade goods. As iron production expanded, birch retained a role as a key source of charcoal for smelting, with potash produced as a valuable by-product. However, its high phosphorus content made it unsuitable for high-quality iron production. This contributed to the negative reputation of birch in "Iron Sweden" – a view that became deeply rooted among foresters (Arpi 1959).

[2] Forest land capable of yielding more than one cubic metre of wood per hectare annually (Skogsdata 2024).

During the industrialisation of Swedish forestry in the 19th and early 20th centuries, birch was increasingly viewed as an undesirable species (Valeur 2014). Forest management practices overwhelmingly prioritised Norway spruce and Scots pine, with birch often being removed from the managed stands using any means available, including large-scale herbicide application (Östlund *et al.* 2022). The development of the first pulp mills saw an increase in the use of birch. However, its shorter fibre and resulting lower paper strength limited its use length (Maddox 1924), especially in early papermaking processes that favoured long-fibred softwoods (Valeur 2014). During World Wars I and II, the perception of birch shifted somewhat due to wartime necessity. Birch fuelwood became crucial as fossil fuel imports to Sweden were restricted (Valeur 2014). The post-war period resumed with a new phase in Sweden's forest history. In the 1950s, forestry shifted to the clear-cutting system as the focus was increasingly set to timber production and profitability (Lindahl *et al.* 2017; Östlund *et al.* 2022; KSLA 2024), which resulted in a continued marginalisation of birch in favour of conifers.

It was not until the 1980s that birch began to gain renewed interest as a viable raw material. This shift can be attributed to technological advancements in pulp utilisation (KSLA 2024) or the introduction of environmental objectives that emphasised better biodiversity in forest landscapes (Lindahl *et al.* 2017; KSLA 2024). In addition, the re-emergence of birch breeding as a research and development priority (Danell & Werner 1989a; Stener & Jansson 2005) brought birch, particularly silver birch, back into focus. Despite renewed attention, the industrial role of birch remains modest compared to conifers. Currently, most of the birch wood in Sweden is consumed by the pulp and paper industry. In addition, birch serves a market for sawlogs and fuelwood, including firewood for private households (Stener & Jansson 2005; Woxblom & Nylinder 2010; Fahlvik *et al.* 2021; Felton *et al.* 2021). Contrary to other countries around the Baltic Sea region – such as Finland (Luostarinen & Verkasalo 2000; Koski & Rousi 2005; Viherä-Aarnio & Velling 2017; Haapanen 2024), Latvia (Jansons *et al.* 2011; Gailis *et al.* 2020b), and Lithuania (Araminienė & Varnagirytė-Kabašinskienė 2014) – Sweden has not developed a strong industry for birch veneer and plywood production. Naturally regenerated birch stands, which supply the bulk of Sweden's birch wood, are commonly associated with lower timber quality (Jones *et al.* 2023b), and are often found in mixtures managed primarily for production of coniferous species (Götmark *et al.* 2005; Holmström *et al.* 2021; Lidman *et al.* 2024a). However, continued progress in tree breeding, alongside the production of high-quality timber, could help establish future value chains based on domestically grown.

1.4 Establishment and early management of birch: from seedling to established stand

Establishment and early management are critical phases in the successful development of birch stands. During these stages, silvicultural decisions such as mechanical site preparation (MSP), choice of regeneration material, spacing, and protection against biotic and abiotic stressors may have long-term implications for stand structure, growth potential, and quality.

1.4.1 Regeneration strategies and early management interventions

Forest regeneration success, whether artificial or natural, depends on several factors. However, these approaches differ significantly in complexity, predictability, and required inputs, with natural regeneration often involving greater uncertainty and dependency on site-specific and climatic conditions. In the following chapters, the primary focus will be on planted birch stands, with natural regeneration used as a reference. A comparative overview of these two regeneration methods is presented in Table 1.

Table 1. Comparison of natural and artificial regeneration, where (+) indicates a relative advantage and (–) a relative disadvantage compared to the alternative method. N indicates no clear advantage or disadvantage compared to the alternative method

Aspect	Natural regeneration	Artificial regeneration
Source	Seeds from tree on the site or nearby trees	Planted seedlings or sown seeds
Establishment cost	Lower (+)	Higher (–)
Control over spacing and density	Low (–)	High (+)
Genetic quality	Variable, often low (–)	Improved through selection (+)

Aspect	Natural regeneration	Artificial regeneration
Initial growth	Slower – seedlings must establish and compete with vegetation (–)	Faster – planted seedlings are often larger and more competitive early on (+)
Overall growth and quality	Variable – depends on site conditions and competition (–)	Higher – uniform spacing and improved genetics allow better growth and yield control but are also site dependent (+)
Management intensity	Lower initially, but may require more tending later (N)	Higher initially, with early vegetation control and spacing requirements (N)
Predictability	Lower – subject to seed year variation and unpredictable site factors (–)	Higher – controlled inputs increase predictability (+)
Economic risk	Lower upfront costs but higher uncertainty and long-term variability in yield (N)	Higher initial investment but more predictable returns if establishment is successful (N)

The artificial regeneration cycle typically begins with MSP. In Sweden, on average 85% of intensively managed regeneration sites undergo MSP as a standard practice (Statistikdatabas 2025). MSP is also commonly used when establishing planted silver birch. However, managed silver birch stands represent a much smaller share of total regeneration efforts, and the absolute number of prepared sites for silver birch is significantly lower. This often site-dependent procedure is largely done to reduce pine weevil damage in coniferous stands (Wallertz *et al.* 2018), a concern that may be less relevant for silver birch. Still, it also improves planting efficiency by creating structured planting spots (e.g., mounds or furrows) that facilitate manual or mechanised planting, reduces soil density and increases soil temperature (Örlander *et al.* 1990; Sutton 1993; Folk & Grossnickle 2000; Nordborg *et al.* 2003; Nilsson *et al.* 2010b; Löf *et al.* 2012). Additionally, MSP may reduce competition with field vegetation (Örlander *et al.* 1990; Sutton 1993), decrease insect herbivory, and enhance nitrogen mineralisation (Johansson 1994; Schmidt *et al.* 1996; Nordborg *et al.* 2003; Smolander & Heiskanen 2007). However, the changes in micro-site conditions are known to vary depending on the method used. Mounding, patch scarification, disc trenching, and soil inversion are among the most commonly used MSP methods. For silver birch, it generally improves seedling survival and early growth (Karlsson 2002). Birch seedlings benefit not only from better soil conditions, such as better access to organic material (Karlsson 2002), but also from reduced competition with field vegetation (Karlsson 2002; Hytönen & Jylhä 2013). Nordin *et al.* (2023) emphasised that mounding may not be a suitable option in drier microsites, as it can exacerbate drought stress (Luoranen *et al.* 2018; Häggström *et al.* 2021) and negatively affect birch seedling performance. In a study conducted in Latvia, Dūmiņš *et al.* (2025) found that birch had the best growth potential on trenched sites, while mounding appeared more suitable for Scots pine and Norway spruce by improving root architecture development. The choice of planting spot is therefore crucial to promote successful seedling establishment (Marquis *et al.* 2021). Elevated planting positions may increase drought risk on dry sites, whereas lower planting positions may be favourable in dry environments but increase the risk of waterlogging in humid sites (Örlander *et al.* 1990; Hansson *et al.* 2018), and should therefore be tailored to local site conditions (Nordin *et al.* 2023).

The choice of initial spacing or planting density critically shapes stand structure, influencing early growth dynamics, intraspecific competition, and the timing and intensity of future silvicultural interventions such as pre-commercial or commercial thinning. Planting density for all species, including silver birch, is guided by national forestry legislation, with specific recommendations varying between countries. In Swedish forestry, the common practice involves planting 1800 – 2000 seedlings ha^{-1}, based on the requirement to have at least 1500 main stems per hectare by the time the stand reaches 1.3 metres in height (Skogsvårdslagstiftningen 2022). However, there is flexibility in how these targets are achieved, allowing forest managers to adapt planting density and spacing according to site conditions, management goals, and economic considerations. While higher planting densities increase regeneration costs, they result in greater total stand production but smaller average stem diameters, illustrating a trade-off between cost, yield, and stem size (Smith & Strub 2012). Spacing trials in silver birch have demonstrated that higher initial planting density increases total volume production, albeit at the expense of thinner stems (Niemistö 1995; Daugaviete *et al.* 2011). Denser plantations may also suffer more from early and intra-specific competition-induced mortality (Niemistö 1995;

Smith & Strub 2012), often requiring earlier management interventions such as pre-commercial thinning (PCT).

PCT is crucial from a silvicultural perspective, as it regulates competition-induced mortality by reducing the density of young stands to target levels. It also enables the selection of trees with the highest potential for future quality (Zālītis & Zālītis 2007; Niemistö *et al.* 2008; Holmström *et al.* 2016; Aosaar *et al.* 2024). Timely PCTs can prevent the development of heterogeneous stand structures, where suppressed trees with slender stems and unbalanced crowns are more prone to snow damage (Peltola *et al.* 1997; Peltola *et al.* 1999; Martiník & Mauer 2012; Donis *et al.* 2024). Beyond density control, PCT can be strategically used to steer stand development toward either higher total volume or larger mean stem diameter, depending on management objectives. Simard *et al.* (2004) reported that after five years, total stand volume was 50.2 m^3 in unthinned paper birch (*Betula papyrifera* Marshall) plots, compared with 30.1, 19.0, and 11.9 m^3 in plots thinned to 3000, 1000, and 400 stems ha^{-1}, respectively – nearly a fivefold difference between the control and the heaviest thinning treatment. Conversely, intensive thinning led to significantly larger quadratic mean diameter (QMD; Simard *et al.* 2004).

1.4.2 The impact of cervid-inflicted damage on seedling and sapling development

In Sweden, the four native cervid species are moose (*Alces alces*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), and red deer (*Cervus elaphus*) (Viltdata 2024). Moose are distributed across most of Sweden with varying population densities, whereas roe deer, red deer, and fallow deer are primarily concentrated in the south. These cervid species differ in their diet preferences and foraging behaviour with moose and roe deer feeding primarily on trees, shrubs, and forbs. In contrast, red deer and fallow deer have a larger proportion of grasses in their diet (Illius 2006; Pfeffer *et al.* 2021). However, all four species exhibit seasonal dietary shifts and typically increase their consumption of woody plants during the winter (Spitzer *et al.* 2020).

Damage inflicted by cervids is one of the most significant challenges to the successful establishment and early development of young forest stands (Gill 1992; Lorentzen Kolstad *et al.* 2018; Ara *et al.* 2022), including young silver birch stands. The extent and nature of deer damage are influenced by multiple factors, including tree species and age (Bergqvist *et al.* 2012; Díaz-Yáñez *et al.* 2017), season (Albon & Langvatn 1992; Illius 2006; Wam & Hjeljord 2010), as well as local cervid densities (Angelstam *et al.* 2000; Edenius *et al.* 2002b; Bergqvist *et al.* 2012; Bergqvist *et al.* 2014). The cervid foraging behaviour is further shaped by how their nutritional requirements interact with the availability of forage across the landscape (Spitzer *et al.* 2020). When alternative or preferred food sources are scarce, this balance may result in increased browsing pressure on young forest stands (Wam *et al.* 2010; Felton *et al.* 2020; Pfeffer *et al.* 2021). Cervids prefer the more palatable RASE[3] species (Bergström & Danell 1986), as well as various understory shrub[4] species. Limited availability or spatial concentration of these preferred plant or woody species (Felton *et al.* 2020; Skogsdata 2024) may compel the animals to browse more heavily on commercially important trees like Scots pine (Bergqvist *et al.* 2001; Nichols & Spong 2014; Felton *et al.* 2022) and, to some extent silver birch (Ahlén 1971; Danell *et al.* 1985; Danell & Ericson 1986; Kullberg & Bergström 2001; Persson *et al.* 2007).

The most common types of cervid-inflicted birch damage are browsing of terminal and lateral shoots (Figure 3a; Danell *et al.* 1985; Bergström & Danell 1986; Persson *et al.* 2005), which can occur during both the dormant and active growing seasons (Danell & Ericson 1986). The extent of browsing depends not only on tree species but also the browsing species, as their foraging behaviours and bite sizes differ (Shipley *et al.* 1999). In summer, leaf stripping may also occur (Figure 3b), particularly on saplings (Cederlund *et al.* 1980; Danell & Ericson 1986).

Trampling can cause mechanical damage to seedlings (Figure 3c), particularly where animal activity or population densities are high (Gill

[3] RASE is an acronym used in Swedish forestry to denote four tree genera commonly preferred by cervids: **R**owans (*Sorbus aucuparia*), **A**spen (*Populus tremula*), willows (***S****alg* in Swedish; *Salix* spp.), and oaks (***Ek*** in Swedish; *Quercus* spp.).

[4] To a large extent species in the family Ericaceae such as bilberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*), which are common understory shrubs in boreal forests.

1992; Illius 2006; den Herder *et al.* 2009), with moose being especially impactful (Persson *et al.* 2000). Moose can also break stems, particularly on slender or insufficiently strong saplings (Figure 3d; Gill 1992; Olmsted *et al.* 2020), to access otherwise out-of-reach shoots (Geist 1963). Although less frequent than shoot browsing, bark stripping or gnawing may also occur, particularly during winter scarcity, and is primarily caused by red deer and moose seeking the nutritious inner bark when other forage is limited (Ireland & Ruxton 2022).

Birch, including silver birch, is notably tolerant of cervid-inflicted damage (Ara *et al.* 2022), largely owing to its compensatory ability (Hester *et al.* 2004). Birch's ability to recover from browsing, commonly referred to as compensatory growth, is an intrinsic tolerance mechanism (Hester *et al.* 2006; Persson *et al.* 2007). In the case of silver birch, this is likely attributed to its relatively fast growth rate (Rosenthal & Kotanen 1994). However, it is likely a combination of intrinsic and extrinsic tolerance that determines how much birch can compensate for browsing damage, with species-specific growth traits interacting with environmental factors such as site productivity. This has been shown for other species, including Scots pine (Danell *et al.* 1991; Edenius *et al.* 1995; Wallgren *et al.* 2014). For instance, larger saplings not only exhibit greater tolerance to browsing but may also reduce their long-term vulnerability by eventually outgrowing the browsing window faster. Ultimately, the extent and nature of a tree's response depend on its size and site conditions, but also on the type, frequency, and severity of the inflicted damage (Hjálten *et al.* 1993; Canham *et al.* 1994). Bergstrom and Danell (1987) showed that only the highest clipping intensity in silver birch resulted in significantly shorter saplings compared to unclipped saplings. Similarly, Persson *et al.* (2005) found a threshold response of no effect up to a low-to-moderate level of biomass removal in birch.

Figure 3. Examples of typical damage inflicted by cervids on young silver birch plantations. (a) Repeatedly browsed silver birch resulting in a bush-like multi-stemmed form; (b) silver birch with evidence of leaf stripping; (c) trampled birch and (d) silver birch with main stem breakage. Photos: Andis Zvirgzdins

Browsing damage, depending on its severity, frequency, and timing, causes a range of negative outcomes, from minor growth reductions due to loss of photosynthetic tissue and carbohydrates (Persson *et al.* 2007) to stem deformities, and in severe cases, tree mortality (Bergstrom & Danell 1987; Gill 1992). Repeated browsing can cause external quality defects in birch, including crooks, multi-stems, spike knots bush-like crown structures. Internal issues such as discoloration and decay may develop as a result of repeated injuries or branch breakage (Rea 2011), ultimately reducing timber quality (Luostarinen & Verkasalo 2000). Although Bergquist *et al.* (2009) observed no significant effects on silver birch stem quality under natural browsing conditions, in contrast with the notable impact on Scots pine (Bergquist *et al.* 2009; Wallgren *et al.* 2014; Matala *et al.* 2020), the long-term implications of such damage on birch timber quality and economic value remain poorly understood.

1.4.3 Management strategies for damage mitigation

To mitigate the browsing impacts on commercially important species, including silver birch, a combination of strategies might be required. These range from large-scale landscape planning to targeted, tree- to stand-level interventions, each tailored to local conditions and browsing pressure. Application of repellents on individual trees is a commonly used, albeit costly, practice. In this context, repellents function as a form of artificial plant defence (Stutz *et al.* 2019), deterring browsing through visual, olfactory, or taste-based cues (Burņeviča *et al.* 2023) that decrease a plant's desirability (Nolte 1998). However, repellents offer only short-term protection. Their effectiveness lasts two to three months and rarely exceeds six months, as they are gradually diminished by weather exposure depending on the specific formulation used (Burņeviča *et al.* 2023). Repeated application may be required depending on the circumstance, and their success is influenced by a range of factors. These include how attractive the target plant is to browsing animals, the density of the local cervid population, the availability of alternative forage, weather conditions, application rates and concentration of the repellent, and how long the treatment remains effective in the field (El Hani & Conover 1995).

Alternatively, physical barriers like stem guards may be used to protect seedlings or saplings against deer. However, barriers protect only a certain part of the tree (Burņeviča *et al.* 2023), leaving the other parts unprotected. Such protection measures are seldom used for birch. Using paper tape was tested on Norway spruce and Scots pine seedlings in Sweden and was applied to protect the leading shoots from browsing damage (Bergquist & Örlander 1996; Bergquist *et al.* 2003b). As evidenced in Bergquist and Örlander

(1996), freeze tape[5] showed significant deterrent effects on browsing of coniferous seedlings. At the stand level, fencing is the most reliable method for safeguarding seedlings (Parker *et al.* 2020), especially when deer population densities are very high. Fences can be made from a variety of materials, including wire or mesh (Redick & Jacobs 2020). Fences can also be installed for a limited time (Bergquist *et al.* 2009) or until the silver birch has escaped the browsing window and the risk of browsing has become negligible. However fencing is a relatively expensive protection method (Burņeviča *et al.* 2023), especially with larger areas to protect.

1.5 Silviculture and management of planted birch stands from young stand to final felling

As a silver birch stand matures, silvicultural decisions, such as thinning regimes, rotation length, and timing of the final felling, must be adapted to site conditions, management goals and market considerations.

1.5.1 Thinning strategies and stand development

Thinning is a fundamental silvicultural intervention that shapes the development trajectory of birch stands by regulating competition and enhancing growth of remaining stems, thereby influencing future stand quality (Hynynen *et al.* 2010; Dubois *et al.* 2020). Thinning strategies in silver birch stands are influenced by both management goals and the stand's initial or realised density, which together determine the timing and intensity of interventions. Under business-as-usual management (stands with 1600 stems ha^{-1}), the first thinning is typically carried out when the stand reaches a dominant height of 13 – 15 metres (Niemistö *et al.* 2008; Hynynen *et al.* 2010; Martiník & Matoušková 2025; Niemistö & Huuskonen 2025). As a comparison, in denser stands with 2500 stems ha^{-1}, the first thinning is likely to be required when the stand reaches 12 – 13 metres in height (Niemistö *et al.* 2008). Naturally, on more fertile sites like former agricultural lands, stands may reach the appropriate thinning stage faster. Liepiņš *et al.* (2013)

[5] Freeze tape (Swedish: *frystejp*) is a tape originally intended for sealing and labelling freezer bags, but it has also been tested as a mechanical browsing repellent.

reported that on former agricultural sites, the first thinning can typically occur between 10 and 12 years of age, or once the stand reaches approximately 12 metres in height. The post-thinning density generally ranges between 700 – 800 stems ha^{-1} under business-as-usual management scenario (Hynynen *et al.* 2010). At a dominant height of 14 metres, young stands typically yield around 30 – 40 m^3sk ha^{-1} (Niemistö *et al.* 2008; Hynynen *et al.* 2010), the majority of which is pulpwood at the time of first thinning (Figure 4). The second thinning typically follows after 10 – 15 years – or at an approximate dominant height of 20 – 22 m – further reducing the density to 350 – 400 trees ha^{-1} (Grīnvalds *et al.* 2008; Hynynen *et al.* 2010). Generally, the second intervention results in a harvested volume of about 70 m^3sk ha^{-1} (Hynynen *et al.* 2010). Under the business-as-usual management scenario, stands undergo two thinnings of moderate intensity, ultimately resulting in a final density of approximately 350 – 400 stems ha^{-1} before the final felling. Ultimately, the exact timing and intensity of these thinnings will vary depending on management objectives, particularly whether maximising diameter growth or total volume production is the main goal.

Figure 4. Birch pulpwood harvested during first thinning. Photo: Andis Zvirgzdins

The trade-off between diameter growth and total volume production depends on thinning practices (Martiník & Matoušková 2025), or more fundamentally, stem density at a given site and age (Assmann 1970). For birch, including silver birch, the general theory is confirmed by existing research, with studies showing that higher-intensity thinning promotes faster individual stem diameter growth (Cameron *et al.* 1995; Skovsgaard *et al.* 2021; Martiník & Matoušková 2025), while higher densities tend to enhance overall stand volume production (Niemistö *et al.* 2008; Hynynen *et al.* 2010; Martiník & Matoušková 2025; Niemistö & Huuskonen 2025). Beyond that, the timing of thinning interventions is crucial. Delayed thinning can harm a stand's long-term growth potential (Rytter 2013) because the response to silvicultural interventions depends heavily on competition within a stand (Lee *et al.* 2025). Timing may also be important in determining the thinning frequency as broadleaved trees, including silver birch, tend to grow fastest immediately following thinning. Rytter and and Werner (2007) observed that diameter growth responses to thinning in multiple broadleaved species were short-lived, with differences diminishing as early as the first year after treatment. Similarly, Erdmann *et al.* (1975), reported that the growth benefits of crown release in yellow birch (*Betula alleghaniensis* Britton) trees lasted about three years before diminishing as crown closure resumed. However, there may not be a single optimal thinning regime for silver birch, as multiple approaches can yield satisfactory outcomes depending on site conditions and management objectives. For instance, moderate and heavy thinnings can result in comparable levels of commercial wood production (Niemistö & Huuskonen 2025). Furthermore, Ahtikoski *et al.* (2004) concluded that a wide range of thinning intensities can support good stand development with similar financial outcomes.

1.5.2 Rotation length in relation to economic and risk considerations

A stand is often considered harvestable when the trees reach the desired dimensions for high-quality timber. The most desirable end product for silver birch is large-dimensioned, straight stems suitable for veneer or sawlogs (Niemistö *et al.* 2008; Verkasalo *et al.* 2017). Birch can reach a mean DBH of 30 cm within 40 – 45 years on high production sites, or 50 – 55 years on less productive sites (Cameron 1996). By applying crop tree silviculture, it may be possible to produce high-value birch timber with a DBH of 45 – 50 cm within a forest rotation of about 50 – 60 years (Hynynen *et al.* 2010;

Dubois *et al.* 2020). Achieving such outcomes requires specific and well-executed silvicultural practices, as well as favourable conditions with absence of browsing and other damage. Timely thinning and early crown release not only promote diameter growth of individual trees but it can also significantly influence the final felling age (Dubois *et al.* 2020).

Forest regulations in some countries specify a minimum final felling age or prescribe harvesting based on a target diameter threshold. However, regulations vary between countries. Silver birch generally has a shorter rotation period than conifers due to an earlier decline of growth (Agestam 1985; Huuskonen *et al.* 2023). In countries specifying a minimum final felling age, it is often determined based on site index (SI), which serves as a proxy for site productivity. For example, in Latvia, the minimum felling age for birch on forest land ranges from 51 to 71 years depending on SI. Contrary to birch grown on forest land, birch plantations (often established on former agricultural lands) are exempt from several legal constraints specified in the law, including the minimum felling age (Law on Forests 2000). In Sweden, the Forestry Act specifies a minimum felling age of 35 years for birch (Skogsstyrelsen 2025). In contrast, optimal rotation age is often determined based on economic criteria, such as maximising net present value (NPV) or land expectation value (LEV), by taking into account growth rates, timber quality, market conditions, and notably the discount rate (Chladná 2007; Klemperer *et al.* 2022). Where there is an established market for birch veneer, the potential value of high-quality birch logs combined with timely management substantially affect both rotation length and overall economic returns (Zeltiņš *et al.* 2025). When such markets are absent, management may prioritise volume production over quality, often resulting in longer rotations. However, silver birch is known to be susceptible to wood coloration and fungal decay (Verkasalo *et al.* 2017; Ciseļonoka *et al.* 2025), so longer rotations may further increase the risk of wood depreciation (Dubois *et al.* 2020).

1.6 Modelling of growth in forest management

Modelling is a central tool to support forest management decision making (Ahtikoski *et al.* 2012; Burkhart & Tomé 2012a; Goude *et al.* 2022). Growth models can operate at either a stand or individual tree level, depending on the detail required (Pretzsch 2009a). Stand-level models provide estimates of aggregate stand characteristics such as total volume, basal area, number of trees per unit area, height, etc. (Vanclay 1994; Weiskittel *et al.* 2011; Burkhart & Tomé 2012b). Growth and yield tables are considered the earliest form of stand-level growth models developed for pure forest stands (Pretzsch 2009a). Individual-tree models, in contrast, focus on the dynamics of single trees within a stand, accounting for attributes such as diameter, height, crown ratio, and spatial positioning. These models allow for a more detailed simulation of stand development by incorporating variation in tree size, species composition, and competition among individuals (Vanclay 1994; Weiskittel *et al.* 2011).

Models can differ also in the underlying data approach, ranging from empirical models based on field measurements to process-based models simulating physiological mechanisms (Vanclay 1994). While mechanistic or physiological models can simulate growth processes by incorporating light, temperature, and soil characteristics (Vanclay 1994), empirical models are purely data-driven, relying on field measurements to predict growth outcomes without explicitly modelling underlying biological processes. Empirical modelling approaches remain the most widely applied in operational forest management.

Empirical forest growth models vary considerably in their statistical formulation, differing in complexity, management accounted for, data requirements, and ease of use (Goude *et al.* 2022). From simple linear regressions to more advanced nonlinear regressions, mixed-effects models and generalised algebraic difference approaches (GADA). Linear regression models are often used due to their simplicity, reliability, and flexibility in incorporating management-related variables, making them effective tools for predicting stand development (Vanclay & Skovsgaard 1997; Weiskittel *et al.* 2011). Nonlinear models are particularly suited for capturing the sigmoidal nature of biological processes like tree and stand growth (Pretzsch 2009b; Weiskittel *et al.* 2011). Mixed-effects models, on the other hand, account for both fixed and random sources of variation, improving accuracy when using hierarchical data (Sharma *et al.* 2019), varying or repeated measures data (Kuehne *et al.* 2022). Frameworks like GADA further enhance flexibility by allowing site-specific growth trajectories and polymorphic growth curves (Burkhart & Tomé 2012c). GADA has been extensively used to estimate base-age invariant height or dominant height-age relationships (Cieszewski 2001; Cieszewski & Strub 2008; Nunes *et al.* 2011; Sharma *et al.* 2011; Ahtikoski *et al.* 2012; Liziniewicz *et al.* 2016; Manso *et al.* 2021; Subedi *et al.* 2023; Stefanello *et al.* 2024; Zeltiņš *et al.* 2024). It has also been used in modelling other silvicultural attributes, including stand basal area (Castedo-Dorado *et al.* 2007).

Nowadays, many models are integrated into advanced forest decision support systems which simultaneously simulate multiple stand-level processes such as growth, mortality, regeneration, and yield under different management scenarios, e.g., Heureka (Wikström *et al.* 2011; Fahlvik *et al.* 2014; Lämås *et al.* 2023) and MOTTI (Salminen & Hynynen 2001; Salminen *et al.* 2005).

1.6.1 Development of growth and yield models for silver birch in Swedish forestry

The first birch yield tables and much subsequent progress in modelling originated from northern Europe. Countries like Finland, Sweden, and Norway have played a leading role in developing growth and yield models tailored to local conditions and management practices (Hynynen *et al.* 2010). In Sweden, the first models developed for silver birch described yield and SI (Fries 1964), followed by stand-level prediction functions for gross basal area growth, stand volume, mortality and ingrowth both for pure and mixed species stands with Norway spruce and Scots pine (Agestam 1985; Ekö 1985). Subsequent research has continuously advanced the dynamic modelling of silver birch in Sweden, focusing on SI models for birch on forest land (Eriksson *et al.* 1997; Johansson 2006) and former agricultural land (Karlsson *et al.* 1997), functions for biomass and tree component allocation (Marklund 1988; Johansson 1999; Claesson *et al.* 2001; Petersson & Ståhl 2006; Johansson 2007), and individual-tree models (Söderberg 1986; Fahlvik & Nyström 2006). However, most of these models are based on data from mixed species stands where birch is not always the dominant species. While many existing functions remain valuable for predicting growth and yield, there is a growing need for new models specifically calibrated for improved, pure silver birch plantations (Zeltiņš *et al.* 2024), especially functions that could be implemented in decisions support systems like Heureka.

2. Thesis aim

This thesis serves as a comprehensive overview of key questions related to the forest management cycle of planted birch in Sweden. Through five studies, the thesis explores diverse but complementary aspects of planted birch management, providing an integrated perspective on sustainable cultivation practices, and contributing to current discussions on browsing impacts and the choice of birch in Swedish forestry (Figure 5).

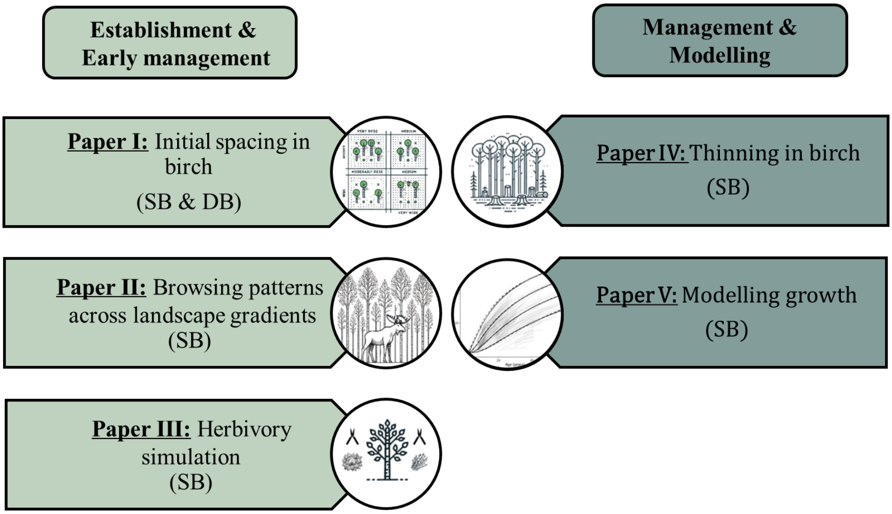

Figure 5. Schematic diagram of the studies included in this thesis, organised according to their thematic focus. The studies are grouped into two overarching categories: (1) establishment and early management, and (2) management and modelling. Each paper addresses different aspects of planted birch silviculture, covering silver birch (SB) and, where applicable, downy birch (DB).

In the context of increasing timber demand and the range of potential management alternatives available for birch, optimising the planting process is essential. **Paper I** investigates the effects of initial spacing and tree density on diameter growth and total production in silver birch and downy birch. The study provides crucial data for improving early stand design, and balancing regeneration cost and productivity with large diameter, high quality birch timber.

Establishment remains a critical phase in birch silviculture, particularly due to the species' vulnerability to browsing damage by large herbivores. This is recognised as one of the major obstacles to successful regeneration of broadleaved species in Sweden. **Papers II** and **III** specifically address these challenges, examining both the patterns of herbivory across landscapes and the consequences of simulated browsing on tree growth and survival. The research questions were formulated to reflect these pressing concerns and provide insights that could inform both site-level decisions and landscape-level applications.

Beyond establishment, long-term production and stand development are critical to sustainable birch management. **Paper IV** evaluates the effects of thinning regimes, contributing to the broader understanding of how intermediate interventions affect individual tree performance and overall stand growth. Lastly, **Paper V** addresses this by modelling growth in improved silver birch plantations, offering new functions for predicting basal area development. These models may be utilised in support planning and decision making by forest managers.

2.1 Objectives

Reflecting this thesis' emphasis on both the early establishment phase and long-term silvicultural management, the specific objectives were formulated as follows below.

Based on Papers I, II and III:

I. To assess how initial density, landscape context and herbivory pressure collectively influence early stand establishment, growth, and quality in silver birch. This objective addresses the need for optimised establishment strategies in a varied and intensively managed landscape, where maintaining a sufficient number of high-quality stems for future processing is a key silvicultural goal.

Based on Papers IV and V:

II. To evaluate how alternative thinning regimes influence stand development and productivity in silver birch plantations, using predictive modelling and economic assessment as supporting tools. This objective integrates practical silviculture – through the application of different thinning regimes – with advanced growth modelling and genetic considerations, aiming to enhance productivity, economic return, and support operational decision making in birch forestry.

3. Materials & methods

3.1 Study description: data and design (**Paper I-V**)

The studies included in this thesis were based on data from short- and long-term controlled experimental trials[6] (Papers I, III, IV and V) and a short-term survey of practical plantations (Paper II). Due to a range of factors, including project timelines, treatment objectives as well as available resources, the experiments showed considerable variation in their number, structure and longevity (Table 2). Papers I and III were based on single-site experiments, whereas Papers II, IV and V were based on data from multiple sites. All study sites were located in Sweden, with the exception of Paper IV, which also included sites in Latvia (Figure 6).

[6] Controlled experiments, in the context of this thesis, refer to field trials in which key treatment factors (e.g., spacing, browsing, or thinning) were deliberately applied according to a structured experimental design, typically involving replication and randomisation.

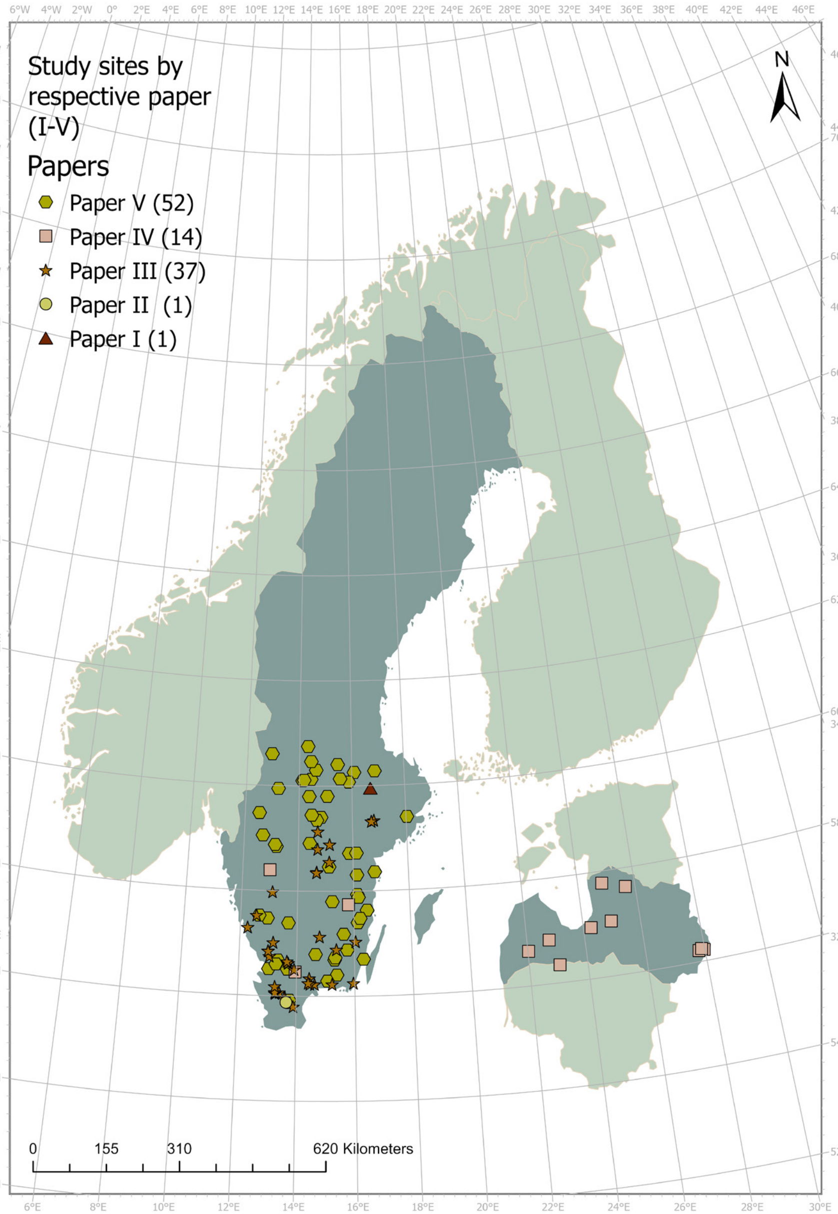

Figure 6. Geographical distribution of study sites from Papers I – V. Most sites are concentrated in southern and central Sweden, with additional sites for Paper IV in Latvia. Each symbol represents one study site, with the number of study sites per paper indicated in the legend.

Table 2. Overview of the studies included in this thesis

Paper	Focus	Species	N of sites (country), land use	Age at last measurement (years)	Experimental design	Plot size	Data acquired
I	Establishment (spacing)	Silver birch, downy birch	1 (Sweden); abandoned agricultural land (AAL)	33 – 34	A single site/block experiment with plot replicates within sites/blocks.	0.00608 – 0.02434 ha	Height (H), diameter at breast height (DBH) (2005 – 2022), height of the live crown (HLC) (2017, 2022)
II	Establishment (browsing)	Silver birch	37 (Sweden); forest land (F)	<15	Survey-based. Circular sample plots & semi-structured interviews	0.0028 ha	H, DBH (2022), tree quality assessment (2022), qualitative data from interviews (2021-2022)
III	Establishment (browsing)	Silver birch	1 (Sweden); F	5	A randomised (row-like) block design (RBD)	Single-tree plots	H, ground level diameter (GLD), tree vitality (2021 – 2023), tree quality assessment (2024)
IV	Management (thinning)	Silver birch	3 (Sweden), F & AAL; 11 (Latvia), F & AAL	17 – 30	RBD with variation in number of replicates per site	0.0452 – 0.21 ha	H, DBH (varying: 2000–2025 at max 2 – 5-year intervals), HLC for series I (2018, 2021, 2023)
V	Management (modelling)	Silver birch	52 (Sweden); F & AAL	21 – 63	Varying (from single tree plots to RBD)	0.04 – 0.1 ha; single tree plots	H, DBH (1990 – 2010)

3.1.1 Controlled field experiments (**Papers I, III, IV**)

The spacing experiment (Paper I) was established to evaluate spacing's impact on silver and downy birch growth and production in a controlled field setting. Both species were planted under four treatments (1.3 × 1.3 m, 1.5 × 1.5 m, 1.8 × 1.8 m, and 2.6 × 2.6 m), corresponding to plot sizes of 13 × 13 m, 15 × 15 m, 18 × 18 m, and 26 × 26 m, respectively. Each treatment was replicated four times per species, resulting in 32 single-species plots, 16 per species, spanning approximately 1.2 hectares. All plots were established with 100 seedlings. Due to logistical constraints, the positions of the plots were predetermined, while species assignment within those plots was randomised. To minimise browsing pressure, particularly from moose, an electric fence was installed around the site before the experiment. In addition, supplementary protection measures were applied to protect the newly planted seedlings from rodents.

The herbivory simulation study (Paper III) was established as a short-term experimental trial to investigate the effect of varying browsing intensities on vitality, growth and quality of silver birch. Prior to planting, the soil was prepared using patch scarification. Just under 1000 silver birch seedlings from the Ekebo 5 orchard were planted in a row-like randomised block design, with each row containing 14 seedlings. Different modes of damage type, browsing intensity, frequency and timing were tested (Table 3). Depending on the season, the treatments were divided into two main classes: 1) clipping shoots during winter and 2) stripping leaves during summer. A total of 13 different treatments, including a replicated control treatment, were randomly assigned to the rows.

Table 3. Treatments and treatment groups

Treatment factor	**Control treatment**	**Treatment groups**		
Intensity (TS – top shoot clipped, SS – side shoot clipped, TS-SS – top and side shoots clipped); Leaf stripping (LLS – light leaf stripping, MLS – moderate	0	TS, SS or TSSS	LLS or MLS	EH

Treatment factor	Control treatment	Treatment groups					
leaf stripping); Extra heavy treatment (EH)							
Timing (WB – winter browsing, SB – summer browsing)	0	WB		SB		WB+SB	
Duration (no. of years treatment was conducted)	0	1	2	1	2	1	2

The thinning trials (Paper IV) were established to evaluate various thinning regimes' impact on growth and volume production. The trials were established both in Latvia and Sweden and varied in site conditions, age and year of establishment. For clarity, the experiments were divided into three series. Series I consisted of thinning trials established in Latvia in 2018. Series II includes trials established in Latvia between 2011 and 2018. Series III consisted of thinning trials established in southern Sweden between 1995 and 1999. In Series I, six target thinning density treatments were applied, including an unthinned control (1200 stems ha^{-1}) and five thinning intensities: 400, 530, 600 and 800 stems ha^{-1}, where the number denotes the target number stems ha^{-1} after the first thinning. The thinnings were applied once between 2017 and 2018. Series II replicated six treatments across multiple sites, using a fixed set of post-thinning densities (e.g., 600, 800, 1000, 1200 stems ha^{-1}), with thinning conducted between 2011 – 2018, depending on site. Series III involved four long-term treatments: two light thinnings (2L), two moderate thinnings (2M), three light thinnings (3L), and two heavy thinnings (2H), reflecting combinations of intensity and frequency. Across all series, thinning intensity could be expressed as the proportion of basal area removed during the first thinning, ranging from 17% in the lightest treatments up to 64% in the most intensive.

3.1.2 Quantitative and qualitative insights into silver birch plantation practices (**Paper III**)

Paper III was based on a mix of semi-structured interviews and field inventories, providing both quantitative and qualitative data. The aim of this study was not only to quantify browsing damage in practical birch plantations across southern Sweden, but also to explore the underlying perceptions guiding decisions to plant birch, and to assess how surrounding landscape characteristics influence damage levels in silver birch plantations.

The first stage of the study consisted of interviews with private forest owners in southern Sweden. Owners were selected based on the following criteria: 1) they had established silver birch plantations within the past decade, and 2) the area of the stand was at least 0.5 ha. Following the selection phase, the owners were contacted by phone and interviewed about their forest estate, their reasons for choosing birch, and their experiences with browsing damage, tree quality, and any protective measures undertaken. The interviews were conducted between autumn 2021 and spring 2022.

Following the first phase, the list of stands was supplemented with additional stands obtained from a database provided by Sveaskog. They were selected using the same criteria as for the private owners, resulting in a total of 37 silver birch plantations. A total of 253 sample plots systematically placed within the selected stands were inventoried in spring 2023. The number of plots per stand depended on stand size and homogeneity, ranging from 4 to 12. Smaller and more homogeneous stands typically required fewer plots, whereas larger and more heterogeneous stands were assigned more plots to capture variability.

3.1.3 Quality assessment (**Papers II & III**)

An important component of the work in Papers II and III was assessing silver birch sapling quality. In both studies, a specific scale was developed or specific quality traits assessed. In Paper II, both stem and crown quality were assessed using a five-point scale, where (I) represented the best quality and (V) the poorest. Crown classes ranged from (I), a top-oriented stem with a clear apical leader, to (V), a bushy or dissolved structure with no dominant shoot. Stem classes ranged from (I) straight, to (V) bent. In Paper III, based on the observations made in the field, four quality classes were defined: 1) trees with no quality issues (straight stems and proportional crowns), 2) trees with bends, 3) trees with spike knots, and 4) trees with forks (Figure 7).

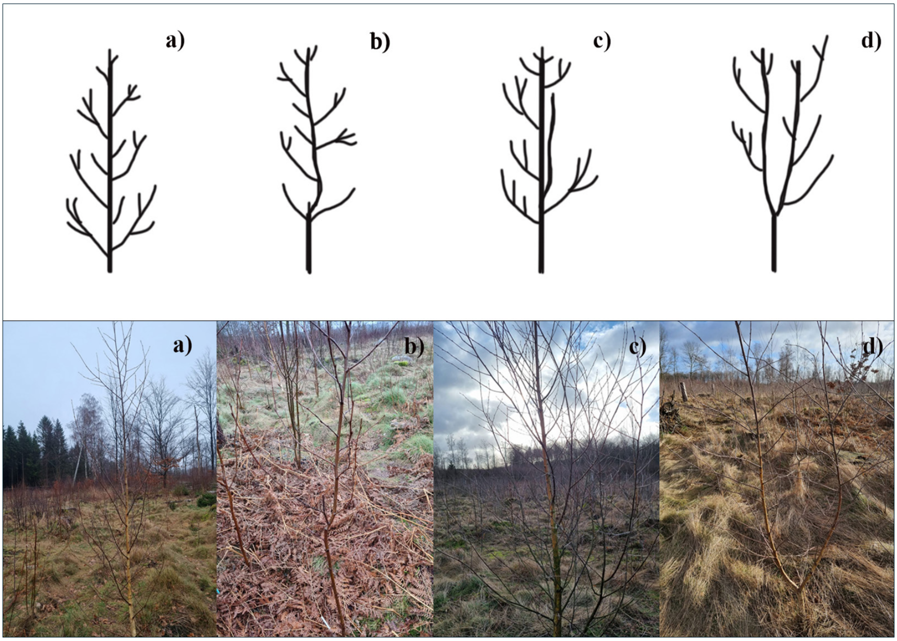

Figure 7. The tree quality classification used in Paper III. a) Trees with no visible defects (straight stems and well-balanced crowns), b) trees with stem bends, c) trees with spike knots, and d) trees with forked stems. Photos: A. Zvirgzdins

3.2 Analysis

This thesis incorporates a diverse set of analytical approaches, ranging from classical inferential statistics and explanatory modelling (Paper I – IV) to predictive growth modelling (Paper IV – V) and qualitative content analysis (Paper II). Suitable methods were selected for each dataset, based on the structure of the experiments and the specific research questions addressed. In Paper III, the models were decided *a priori*, whereas in Papers I, II, IV and V, model selection involved data-driven comparison of candidate models. Candidate models were compared using graphical inspection and when applicable, statistical tests such as the Shapiro-Wilk test (Shapiro & Wilk 1965) were used for assessing normality of the residuals. To improve normality and meet model assumptions, various data transformations were applied, including logarithmic, square root and sine transformations.

Explanatory modelling was the most common modelling approach in this thesis. Frequently applied explanatory modelling methods included analysis of variance (ANOVA), linear mixed-effects models (LMM), generalised linear models (GLM), and generalised linear mixed-effects models (GLMM), depending on the structure of the data and the research question (Table 4). ANOVA (type III) was used when assessing effects of different silvicultural treatments, such as spacing or thinning. Subsequently, pairwise comparisons of estimated marginal means (EMMs) were typically conducted using the Tukey test with a 95% confidence level, applying Tukey-adjusted p-values to account for multiple comparisons. To handle more complex data structures, mixed-effects models (LMM and GLMM) were applied to account for the hierarchical design and repeated observations. GLMs and GLMMs were applied to datasets where the response variable did not follow a normal distribution, including binary (presence-absence data) and proportional outcomes (level of severely damaged trees in a stand). In such cases, a logit link was selected for models with a binomial distribution. Lastly, to compare the proportions of each land cover class between stands, a Welch's t-test (Welch 1947) was applied. Predictive models were developed in Papers IV and V, to estimate stand-level development from key structural variables and management regimes. Such models included LM, LMM, and GADA-based dynamic equations, and they are described in detail in the following chapter. Model accuracy in Paper V was assessed using root mean squared error (RMSE), mean absolute error (MAE), and modelling efficiency coefficient (ME).

All calculations and modelling were preformed using R, version 4.3.2 (*R Core Team* 2023). GLM and mixed-effects modelling was carried out using glmmTMB (Brooks *et al.* 2017) and lme4 (Bates *et al.* 2015) packages as well as base R.

Table 4. Analytical depth and purpose of analysis used in the thesis.

Paper	Modelling approach	Statistical methods used	Purpose of the analysis
I	Explanatory modelling	LM, Type III ANOVA, Tukey's post hoc test	To test the effect of spacing and species on growth (height, diameter) and to assess treatment-level differences

Paper	Modelling approach	Statistical methods used	Purpose of the analysis
II	Quantitative summary statistics, qualitative narratives		To summarise landowners' perspectives on browsing and birch management.
	Exploratory multivariate analysis	PCA	To summarise landscape structure and address multicollinearity
	Explanatory modelling	GLMM	To test the influence of landscape and stand-level factors on the probability of severe browsing.
		Welch's t-test	To compare browsing intensity between land use classes.
III	Explanatory modelling	LMM	To assess the impact of simulated browsing treatments on height and GLD
		GLM	To model probabilities of the observed quality traits: bends, forks and spike knots
		GLMM	To assess the impact of simulated browsing treatments on sapling mortality
IV	Explanatory modelling	LMMs, Type III ANOVA, Tukey's post hoc test	To evaluate the effect of thinning treatments on growth
	Predictive modelling	LMMs	To develop site-specific functions for basal area, top height and stand-form height.
V	Explanatory modelling	LM	To develop basal area, top height, and form height functions for genetically improved birch.
	Predictive modelling	GADA	
	Validation	RMSE, MAE, ME	To assess prediction accuracy.
	Bias assessment	t-test	To test for systematic deviations (bias).

3.3 Growth modelling

3.3.1 Modelling site-specific basal area, top height and stand-form height (**Paper IV**)

In Paper IV, deviations from the original research plan prevented reporting on individual treatment effects. Instead, the data was re-purposed to estimate three stand-level functions, describing stand BA growth, top height and stand-form height (Figure 8). The functions were developed using an LMM approach, allowing site- and plot-level random intercepts to account for the hierarchical structure of the data. The fixed effects included covariates such as the number of stems, stand basal area, top height and age, with the latter two subjected to transformations (e.g., sine or logarithmic). The three functions were combined with existing mortality models (Siipilehto *et al.* 2020) to simulate volume, QMD and MAI across the four newly defined thinning scenarios.

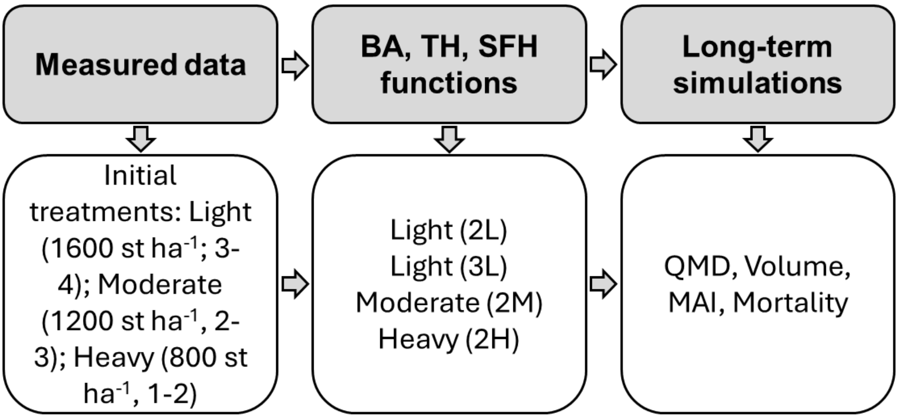

Figure 8. Schematic diagram of the modelling workflow used in Paper IV. Measured data from the initial thinning treatments (light, moderate, heavy) were used to parameterise functions for basal area growth (BA), top height (TH), and stand form height (SFH). Parentheses denote the number of thinnings planned and their intensity: L (light), M (moderate), and H (heavy). The developed functions, combined with existing mortality models, were applied in simulations of long-term stand development under four thinning regimes. Simulated outputs included quadratic mean diameter (QMD), stand volume, mean annual increment (MAI), and mortality – with the latter estimated using already-existing mortality functions (Siipilehto *et al.* 2020).

3.3.2 Modelling basal area and volume for improved silver birch (**Paper V**)

In Paper V, a new stand-level function for predicting basal area (BA) was developed using data from genetically improved birch plantations in southern Sweden. Although the primary objective was to develop a stand-level BA function (BAP), the study ultimately produced a set of models, including BA starting (SV) and volume functions (VF; Figure 9). SV and VF were linear models, developed using data from experimental plots in which the variables were either measured or estimated based on other measurements. BAP was a non-linear dynamic model fitted using the generalised algebraic difference approach (GADA). A total of six functions based on established growth functions, e.g., Korf, Hossfeld, and Bertalanffy-Richards, were fitted using GADA and the dummy variable method (Cieszewski & Bailey 2000), allowing both site-specific parameterisation and application across multiple growth intervals.

The modelling stage was followed by model assessment. The fit of the functions was evaluated both graphically and statistically. Furthermore, the BAP function was validated using an independent dataset from Finland consisting of experiments thinned at different intensities. The validation dataset included twelve different sites, with observation periods ranging from 16 to 48 years. The observed basal area was compared to the modelled values, with model performance evaluated using RMSE, MAE, and ME.

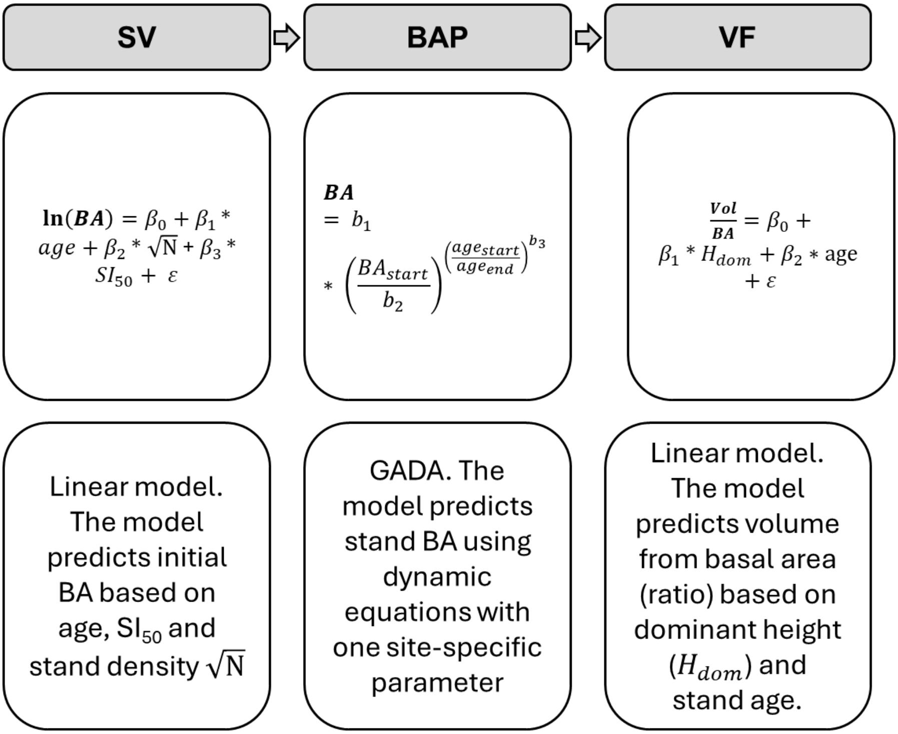

Figure 9. Schematic diagram of the functions used in the development of SV (BA Starting Values), BAP (Basal Area Projection), and VF (Volume Function) in Paper V. SV is estimated using a linear model based on stand age, site index (SI_{50}), and stand density ($\sqrt{N}$). BAP applies a dynamic growth model (GADA) incorporating one site-specific parameter to project stand basal area over time. VF predicts volume per unit basal area as a function of dominant height (H_{dom}) and stand age using a linear regression model.

4. Main Results & Discussion

4.1 Establishment phase: early growth, spacing, and herbivory by cervids

This section examined early growth in relation to spacing (Paper I), the effects of browsing on survival, development, and quality (Papers II – III), and forest owners' strategies for managing risks (Paper II). Together, these studies raise the question: how do spacing and browsing pressure interact during establishment?

4.1.1 Forest owner strategies and perceptions of birch establishment *(**Paper II, interviews**)*

The most important argument for choosing birch among the interviewed forest owners was to adapt to site conditions, such as high soil moisture, and to manage risks associated with Norway spruce. This was followed by a desire to increase tree species diversity, fostering ecologically resilient mixed forests, and to create more visually appealing stands, especially near homes or recreational areas. The exact reasons behind replacing Norway spruce with silver birch were not always stated but discussed were reasons such as storm damage, root rot, and bark beetle infestations. Earlier studies have suggested that the risks linked to traditional conifer management, especially of Norway spruce, have not been perceived as decisive in shaping species selection (Eriksson 2014; Lodin *et al.* 2017). While the insights of this study may indicate otherwise, it is important to note that the forest owners interviewed in this study had actively invested in planting silver birch, reflecting a deliberate and forward-looking commitment to the tree species. They may not be representative of the average or typical forest owner in Sweden. Still, a shift in silvicultural preferences seems to be emerging. This is likely not only due to risks linked to Norway spruce (Keskitalo *et al.* 2016; Subramanian *et al.* 2016; Svystun *et al.* 2021), but also to generational or attitudinal change among forest owners, who may lack traditional forest management knowledge and may be less driven by economic objectives (Lodin & Brukas 2021). Nonetheless, birch is increasingly recognised for its ecological and silvicultural value in Sweden (Lidman *et al.* 2024b). Based on this study, there is a clear and growing interest in planted silver birch as a viable and flexible alternative, both for ecological and practical reasons. Although silver birch remains a small part of total seedling production, its annual output has nearly quadrupled since 2011, increasing from 0.9 million to 3.8 million seedlings in 2024, growing from 0.23% to 0.94% of all seedlings produced (Skogsstyrelsen Statistical Database 2024).

Similarly, interest in planting silver birch may also be constrained by risks, most notably browsing by cervids. However, responses from the surveyed forest owners suggested that browsing pressure was generally perceived as low: half reported no browsing at all, and only 2 out of 28 respondents considered it a serious or very serious problem (Figure 10). Previous studies have highlighted that private Swedish forest owners generally regard browsing damage by deer as a major hazard in young forest stands (Blennow & Sallnäs 2002). Among the many potential explanations, one certainly is that the forest owners in this study had actively invested in planted birch. Many had taken deliberate steps to protect their birch stands, using measures such sheep wool, freeze tape, and odour or taste based repellents. However, while plant protection can reduce browsing risk in young birch stands, other factors, such as local cervid densities and landscape-level forage availability, may ultimately play a more decisive role.

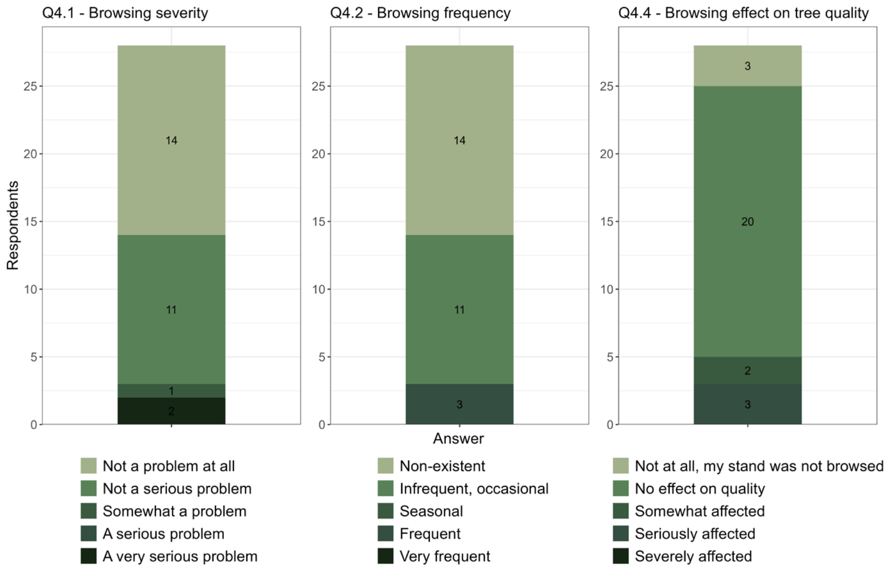

Figure 10. Perceived severity, frequency, and effects of browsing damage on stand development in silver birch. Shown are responses to three survey questions on browsing damage by cervids: (Q4.1) the perceived severity of browsing, (Q4.2) the frequency of browsing, and (Q4.4) the perceived impact of browsing on tree quality. Bar heights show the total number of respondents, with segments coloured by response category.

4.1.2 Survey and landscape analysis of browsing impacts *(**Paper II, survey**)*

Part II of Paper II quantified browsing levels using a large-scale survey. In line with the interview results, the condition of the young birch plantations was generally very good. However, it appeared that forest owners may slightly underestimate the damage, possibly due to gradual damage going unnoticed or the owners having limited means to assess it. In 23 out of the 37 inventoried stands, more than half of the stems were classified as damaged. However, in many of these stands, the overall stem quality remained acceptable (Figure 11). Across all sites, 74% of the stems were categorised as either undamaged or damaged but of acceptable quality, while only 26% were classified as being of poor quality.

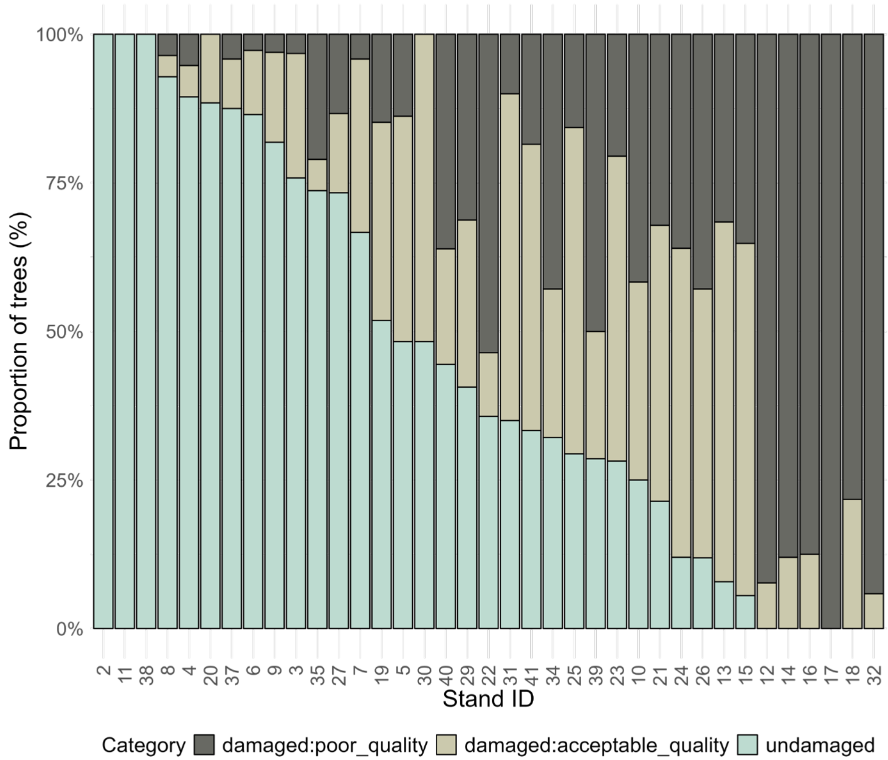

Figure 11. Proportion of trees by damage and quality classification across birch stands. Based on stem and crown assessments, trees were classified as undamaged (no damage observed), damaged with acceptable quality (minor defects in stem and crown: quality classes 1 – 3), or damaged with poor quality (major defects: quality class 4 or 5 in either stem or crown). Each bar represents a single stand (Stand ID), with segments indicating the relative frequency of each category.

The survey study showed that stands with a higher mean tree height generally had fewer visible signs of browsing damage than stands with smaller trees. This indicates that damage sustained in the early stages, especially light damage, may become less apparent as the trees mature. In line with findings on birch trees' tolerance of herbivory, this may suggest that early, and in particular light damage, does not always translate into poor stand quality. Still, it remains unclear how this resilience persists under repeated or severe browsing pressure; neither this nor other studies have investigated long-term impacts of browsing on birch quality. Certainly, where browsing pressure is severe, it is more likely to permanently harm tree quality and stand value. As observed in the survey, a total of six stands were classified as very poor quality, with more than 75% of the trees in these stands falling into the lowest quality category.

Damage in birch and other young stands can be influenced by tree species or stand structure, but also by cervid density, landscape composition, and forage availability. For this reason, a landscape analysis was conducted to complement the stand-level data in Paper II. The analysis revealed that high-damage stands were found in landscapes with more clearcuts and wetlands, while low-damage stands were surrounded by more arable land (Figure 12).

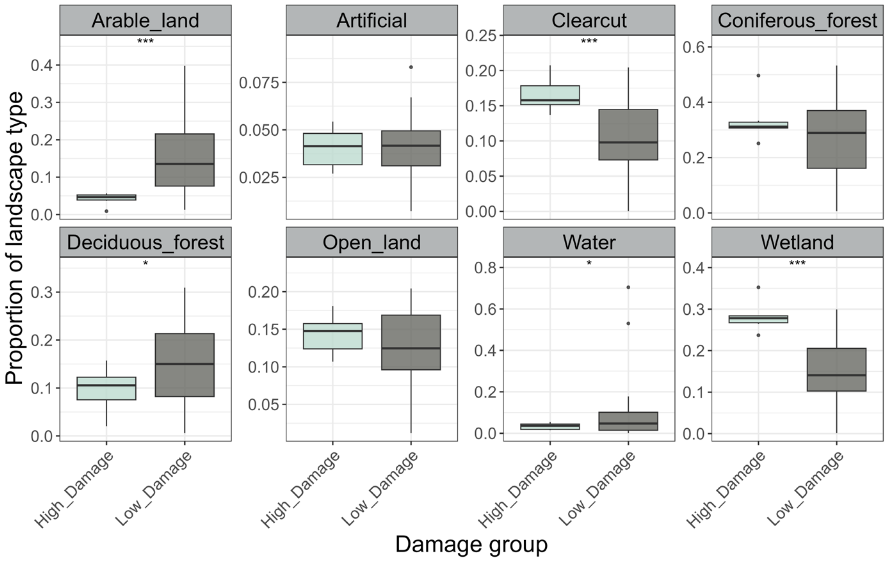

Figure 12. Comparison of landscape composition between high- and low-damage stands. Boxplots show the proportion of each land cover class within 8 km of stands grouped by damage severity. For each variable, the box shows the interquartile range (IQR, 25th–75th percentile), the horizontal line within the box represents the median, and the whiskers extend to the most extreme data points within 1.5 × IQR. Points beyond this range are shown as outliers. Asterisks indicate significance levels from Welch's t-tests comparing group means (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

This suggests that these landscape types offer favourable conditions for large herbivores, either as areas used for forage (Courtois *et al.* 2002; Nikula *et al.* 2004; Osko *et al.* 2004), or as shelter areas, e.g., for thermoregulatory refuge (Laforge *et al.* 2016). Since much of Sweden's forest landscape is intensively managed, often with highly palatable species like Scots pine, using landscape-level information to mitigate or avoid high-damage areas may be challenging.

4.1.3 Simulated browsing and recovery capacity ***(Paper III)***

In Paper III, controlled browsing, performed with a range of clipping treatments, demonstrated that light to moderate browsing does not necessarily kill planted silver birch or slow down its growth. These findings aligns with a 100% silver birch survival rate reported by Bergstrom and Danell (1987). Consistent with the findings of Hjálten *et al.* (1993), birch showed a strong capacity for compensatory growth. This was reflected in the absence of significant height differences between the simulated browsing treatments as demonstrated by the GLMM (Figure 13).

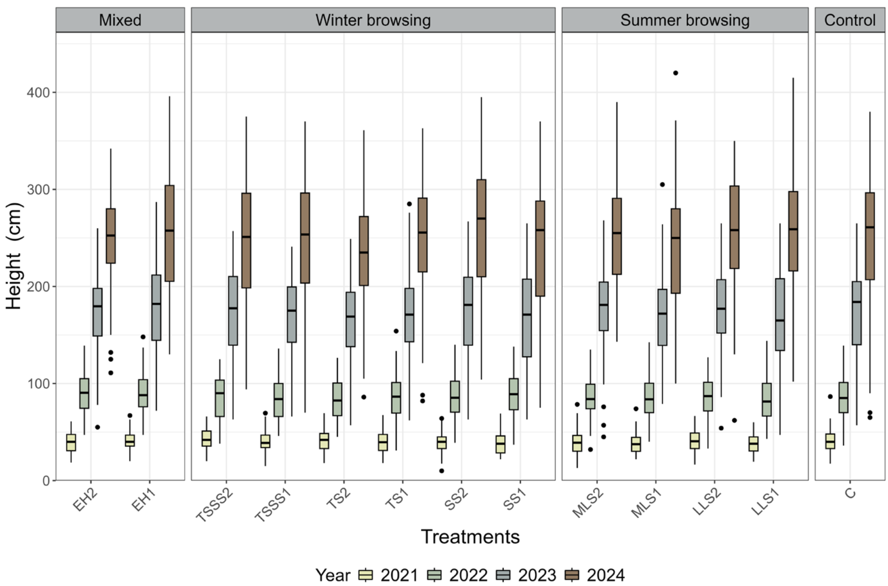

Figure 13. Measured mean height of seedlings planted in Fulltofta across various treatments from 2021 to 2024. Each set of boxes indicates a different treatment group. Sample size per treatment per year: n = 60-71; control: n = 131-141. The groups and treatments within the groups are organised according to an assumed spectrum of severity from most severe (EH2) to least severe (C). The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both top shoot and side shoot clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied). Abbreviations ending in 1 were treated during the first year after planting whereas

abbreviations ending in a 2 were treated for two consecutive years after planting. Boxplots display the median (central line), interquartile range (IQR; the box spans the 25th to 75th percentile), and whiskers extending to the most extreme values within 1.5 × IQR. Points beyond this range represent outliers.

Even when apical dominance was disrupted or when low-level damage was repeated, the trees' growth remained unaffected. However, the disruption of apical dominance had a significant impact on tree quality. The removal of the top shoot for one or two seasons increased the frequency of stem bending (Figure 14).

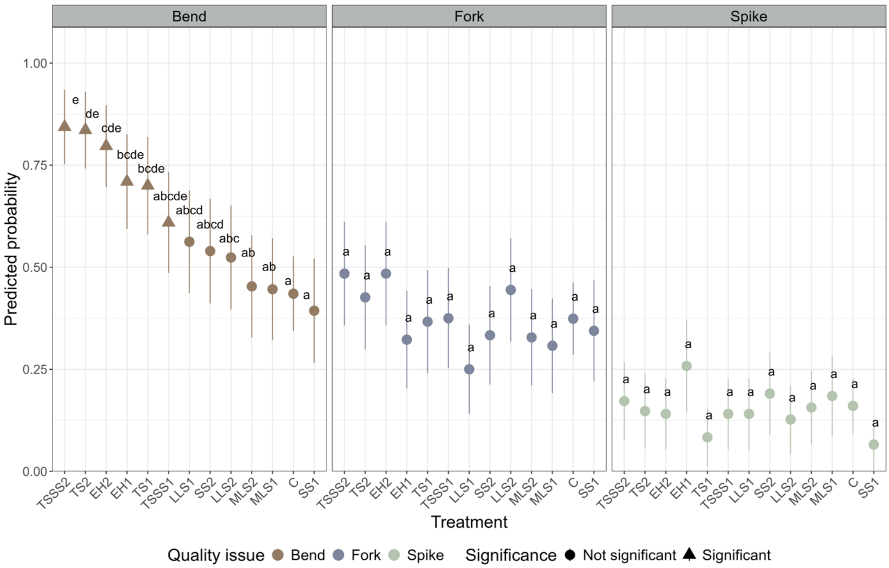

Figure 14. Modelled predicted probabilities extracted from the model and analyzed for significance by pairwise comparisons, accounting for multiple comparisons using a Sidak adjustment. Treatments within each quality issue sharing the same small letter are not significantly different from each other at p<.05. For treatment explanations, see Figure 12. Error bars represent 95% confidence intervals, and letters denote significant differences between treatments within each quality issue.

Aligning with the results of our study, Sisenis *et al.* (2016) reported a significantly negative impact of browsing damage on silver birch quality in plantations in Latvia. As a result of heavy browsing, trees had significantly higher frequency of bends and spike knots. However, repeatedly browsed birch trees may also develop internal quality defects such as discoloration and decay caused by breakage of branches (Rea 2011). Overall, while lightly browsed trees may recover from browsing damage, heavy browsing causes long-term harm to stem form, growth, and quality.

4.1.4 Effect of initial spacing and planting density (**Paper I**)

Planting density impacts in various square-spacing treatments was assessed for both silver- and downy birch on a single site in central Sweden (Paper I). The effect of spacing has been documented extensively for other species, but mostly for conifers, including maritime pine (*Pinus pinaster Aiton*) (Euler *et al.* 1992), lodgepole pine (*Pinus contorta Douglas*) (Liziniewicz *et al.* 2012), Scots pine (Eklund 1956), Norway spruce (Wiksten 1965), and Douglas-fir (*Pseudotsuga menziesii var. menziesii [Mirb.] Franco*) (Peracca & O'Hara 2008). The few studies on birch have shown the expected trend: higher initial planting densities tend to result in greater total volume production, but at the cost of reduced diameter growth compared to lower densities (Niemistö 1995; Daugaviete *et al.* 2011). Our study delivered partially coinciding results. Sparser initial spacings resulted in a significantly higher diameter at the end of the rotation, whereas MAI was significantly affected, but only for downy birch (Figure 15). Accordingly, standing volume was also significantly affected only for downy birch.

Because data from the first thinning were unavailable, it was not possible to validate the actual effect of thinning or evaluate total volume production in the trial. To compensate for the absence of data on thinned volumes, a sensitivity analysis was done to simulate volume removal during the first thinning. Three intensities – 25%, 30%, and 40% of volume removed – were tested by adding simulated thinned volume to the total volume at the final measurement. The 30% scenario is shown in Figure 15. Simulations were applied to all spacing configurations except the 2.6 × 2.6 m spacing, with one exception in downy birch.

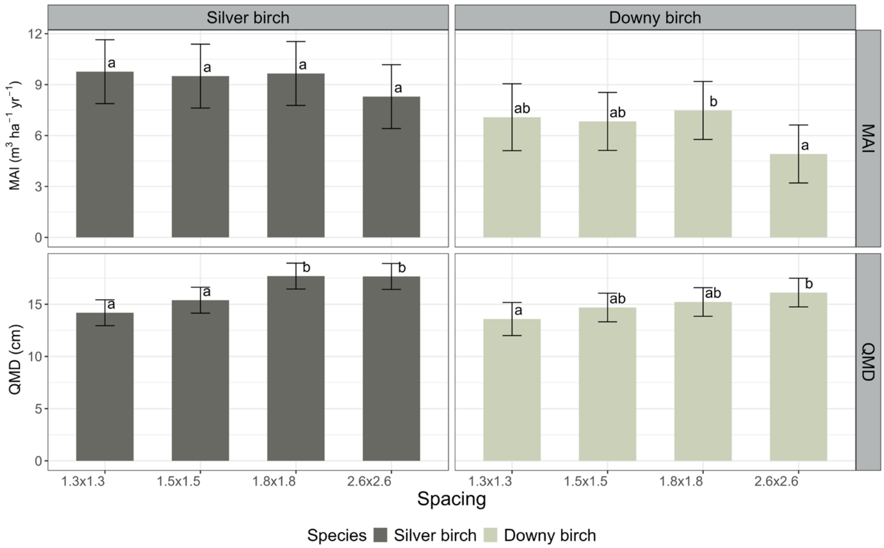

Figure 15. Effect of spacing on QMD and volume growth in silver birch and downy birch over 33 and 34 years respectively. Bar plots showing the estimated marginal means (±95% confidence intervals) of quadratic mean diameter (QMD, cm) and mean annual increment (MAI, $m^3\ ha^{-1}\ yr^{-1}$) at final felling for silver birch (left) and downy birch (right), across four initial spacing treatments. Lowercase letters indicate statistically significant differences between spacing levels within each species and variable (Tukey-adjusted $p < 0.05$).

Spacing had only a limited effect on MAI, particularly for silver birch, where values were similar across spacings. QMD increased consistently with wider spacings, highlighting the trade-off between stand density and individual tree growth. For example, at 1.5 × 1.5 m and 1.8 × 1.8 m spacings, silver birch showed similar MAI, yet the wider spacing produced larger diameters. These results indicate that choosing slightly wider spacings (≥ 1.8 m) can promote individual tree growth without substantially reducing overall production. At the species level, silver birch outperformed downy birch in QMD and volume growth, in agreement with earlier findings (Hytönen *et al.* 2014; Bērziņa *et al.* 2017). Notably, the differences between species in our study were not only due to differences in growth but also possibly due to realized stand density. However, due to the absence of detailed records, it was not possible to determine whether these differences arose from mortality or from thinning.

4.1.5 The interplay between spacing and browsing in early stand development

Planting density can be used as a key silvicultural tool for managing the trade-off between diameter growth and total volume production (Niemistö 1995; Daugaviete *et al.* 2011; Smith & Strub 2012).

However, density may also modulate the effects of browsing pressure by cervids. For instance, Lyly and Saksa (1992) argued that a regeneration density of at least 4000 Scots pine seedlings ha^{-1} is required in areas with repeated moose browsing. The strategy behind increased planting density is that the number of browsed trees increases more slowly than the increase in stem density (Andrén & Angelstam 1993). Lyly and Saksa (1992) showed that, in densities ranging from 2000 to 11,000 Scots pine seedlings ha^{-1}, the proportion of moose-damaged saplings fell from 40% to 20%. Similarly, Bergqvist *et al.* (2014) concluded that damage in Scots pine stands could be reduced by increasing tree density. However, above a certain threshold, the effect might be reverse (Lyly & Saksa 1992), possibly due to moose using the overly dense stands as shelter against predation (Domisch *et al.* 2024).

The interaction between planting density and browsing by cervids in silver birch remains insufficiently studied. By drawing parallels from findings in Scots pine, it can be speculated that increasing silver birch density may also reduce the overall impact of browsing. By increasing initial density, browsing pressure may be distributed across a larger number of stems, thereby reducing individual trees' risk of severe damage. However, planting higher-density stands would further increase establishment costs. Alternatively, a combination of naturally regenerated birch and planted silver birch might offer a cost-effective compromise by enhancing stem density while ensuring the presence of high-quality crop trees. Stands regenerated naturally typically achieve sufficient density at no added cost, and practical experience suggests that dense naturally regenerated birch may help buffer browsing pressure. Naturally regenerated high-density stands would also require more intensive pre-commercial thinning (PCT) to ensure optimal spacing and reduce competition, which may increase management costs in later stages. Furthermore, PCT could potentially be used as a tool to reduce browsing damage impacts in scenarios involving birch. As concluded by

(Fahlvik *et al.* 2018), although delaying PCT may lower economic value, it appears to be a reasonable strategy in naturally regenerated Scots pine stands under high browsing pressure, as allowing the stand to grow beyond the vulnerable browsing stage can ultimately be more cost-effective. While high-density plantations may experience early mortality (Niemistö 1995; Smith & Strub 2012), it typically affects the smallest trees and can even reduce the cost of PCT. Therefore, even though PCT could potentially solve the browsing issue, it must be carefully timed and planned to avoid amplifying other risks like damage from snow (Dreimanis 2016; Donis et al. 2024). However, the above speculations concerning birch remain untested and require further investigation.

4.2 Management phase: silviculture of established stands

Two complementary studies (Papers IV and V) focused on stand development beyond the establishment stage. This raised the question of how thinning strategies and stand-level modelling can be integrated to inform strategies for long-term growth, yield, and potential economic performance.

4.2.1 Effects of thinning intensity and timing on stand development (**Paper IV**)

In monospecific stands, the classic trade-off between diameter growth and total volume production can readily be explained as a function of tree density at a given site (Assmann 1970). This makes thinning to reduce tree density an efficient way to modulate stand development. Simulations of long-term stand development in silver birch showed that the regime with two heavy thinnings (2H) resulted in the lowest total standing volume, whereas two light thinnings (2L) produced the highest standing volume. These findings are well supported by earlier research and literature (Cameron *et al.* 1995; Niemistö *et al.* 2008; Hynynen *et al.* 2010; Dubois *et al.* 2020; Skovsgaard *et al.* 2021; Martiník & Matoušková 2025; Niemistö & Huuskonen 2025). Conversely, QMD followed the opposite pattern, with the largest QMD observed under heavy thinning (2H) and the smallest under light thinning (2L).

The differences between thinning treatments in growth response were most pronounced immediately after thinning (2017 – 2021), with trees in the more intensive treatments (e.g., 400 and 530) growing substantially more than those in lower intensity treatments (e.g., 800 and 1200), an outcome that diminished over time (Figure 16). Furthermore, a pattern in growth rate was also observed between different-sized trees. Trees with larger starting diameters consistently increased basal area faster than smaller trees across all treatments. Given the relatively weak thinning response of silver birch, particularly in terms of diameter growth, and the minimal differences in merchantable timber between moderate and heavy thinning regimes (Niemistö & Huuskonen 2025), it may be reasonable to conclude that standard thinning offers limited silvicultural benefit in silver birch stands. If the management objective is to enhance diameter growth and increase the number of larger-diameter trees at the end of the rotation, heavy thinning may be necessary, albeit at the expense of total volume production. Conversely, a more efficient strategy for pulpwood or biomass production may be maintaining a denser stand with lighter or no thinning and aiming for shorter rotations.

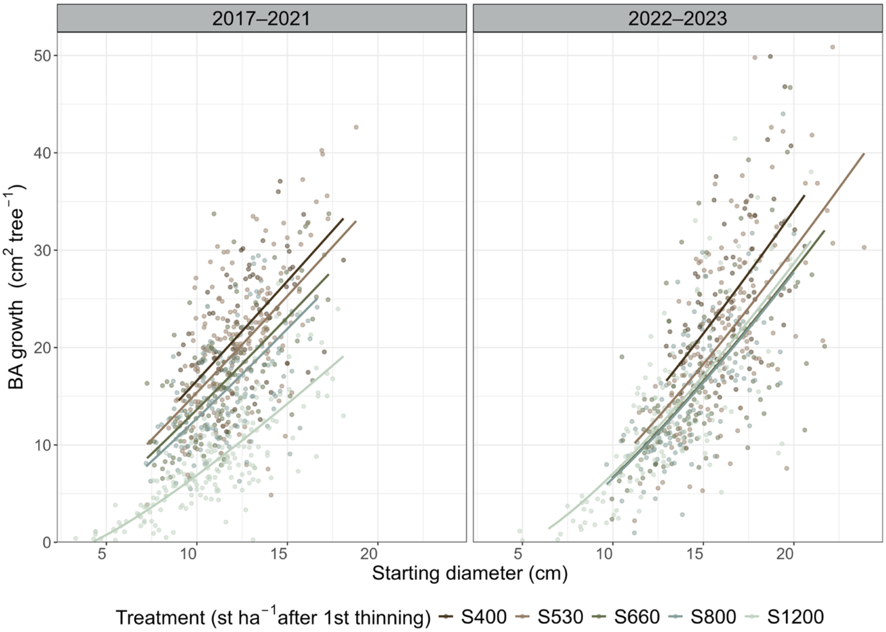

Figure 16. Relationship between starting diameter and basal area (BA) growth (cm^2 $tree^{-1}$) for different thinning treatments across the sites (1 – 3) in series I over two time periods (2017 – 2021 and 2022 – 2023). Lines show treatment-specific linear trends. Treatments indicate post-thinning densities.

4.2.2 Modelling growth in improved silver birch (**Paper V**)

Paper V aimed to develop new basal area functions that could support long-term growth predictions of genetically improved silver birch under varying management regimes. Of all the tested functions, the best fit statistics, graphical agreement with observed data, and model parsimony were achieved by the two-parameter Korf function (Figure 17; BA1), using one site-specific parameter. As the model showcased, the use of genetically improved material can be efficiently accounted for by modifying site index in the SV – the function predicting initial basal area. While applying this approach may require consideration of stability of site index, especially over longer projections, it is straightforward and practical compared to calculating specific genetic gain multipliers or calibrating model parameters (Egbäck *et al.* 2017; Deng *et al.* 2020).

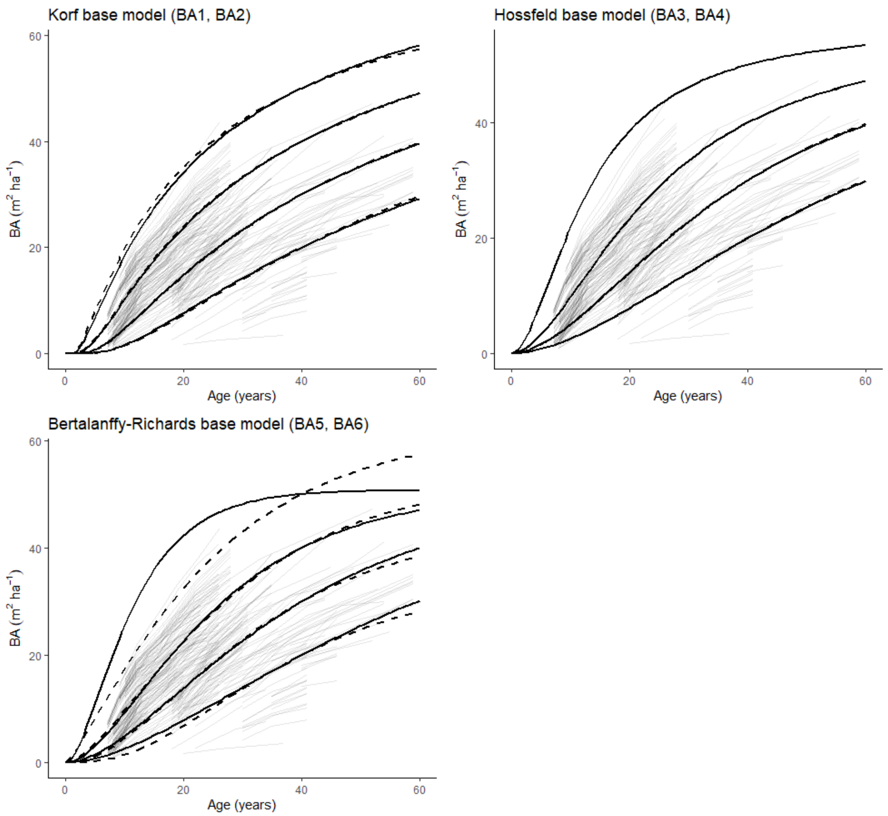

Figure 17. Basal area development curves of silver birch reaching basal areas of 15, 25, 35, and 45 $m^2\ ha^{-1}$ at 40 years for the two-parameter models (BA1, BA3, BA5; solid lines) and the three-parameter models (BA2, BA4, BA6; dashed lines). Gray lines represent measured data.

4.2.3 Simulation of MAI under varying genetic gain and corresponding site productivity in silver birch stands

To explore how genetic improvement may influence productivity, MAI was simulated across different site index classes using the findings from Paper V. Assuming $SIH_{50} = 24$, three levels of genetic gain was calculated responding to $SIH_{50} = 24$, 28 and 32 respectively. Since SIH reflects expected dominant height at the reference age (Goelz & Burk 1992; Skovsgaard & Vanclay

2008; Burkhart & Tomé 2012c), genetic improvement can be incorporated by shifting SI curves upward in proportion to the anticipated genetic gain (Buford & Burkhart 1987). This adjustment allowed simulations of MAI to reflect productivity under both baseline and improved planting material. Each simulation assumed an initial stand density of 2200 stems ha^{-1} at age 10, with a thinning regime consisting of two commercial thinnings, each removing 30% of the basal area. As shown in Figure 18, not only does MAI increase with higher SI or improved genetics, also the maximum MAI comes earlier in the stand rotation.

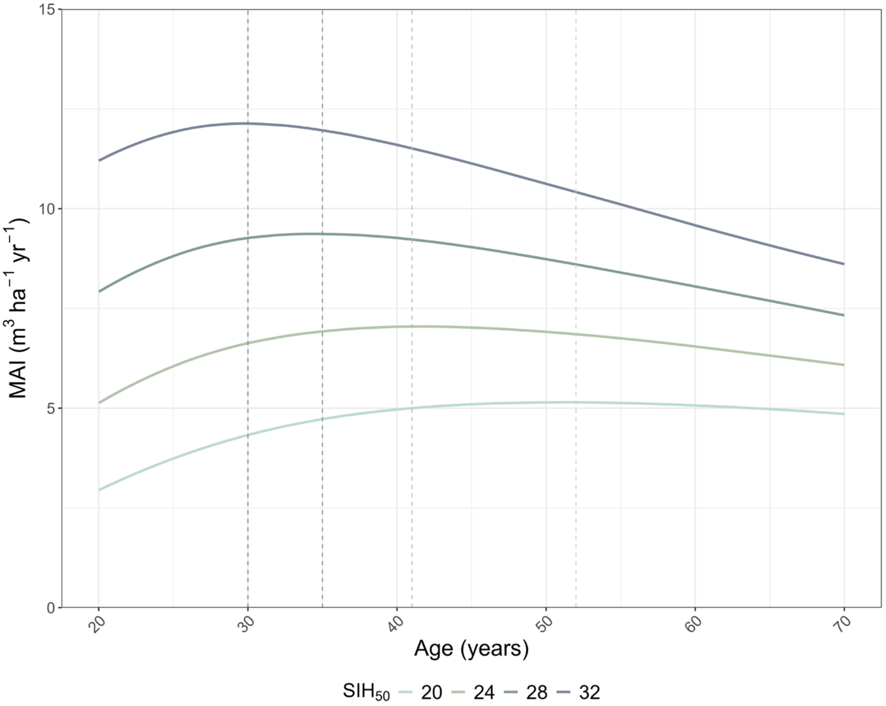

Figure 18. Simulated mean annual increment (MAI) by age for four site index classes (SIH_{50} = 20, 24, 28, and 32) using the basal area model developed in Paper V. Vertical dashed lines indicate the age at which MAI peaks for each site index class.

The model demonstrated a more accurate growth potential for planted silver birch in Sweden, ranging from 5 to 12 m^3 ha^{-1} year^{-1}, compared to earlier estimates based on naturally regenerated birch in survey data (Ekö *et al.* 2008). Furthermore, the level of genetic improvement corresponded with reduced rotation length, in line with (Zeltiņš *et al.* 2025). As shown by Joo *et al.* (2020), the adjustment of SI curves through proportional upward shifts provided results comparable to those obtained with alternative approaches, such as genetic gain multipliers, thereby supporting the validity of the SI method for incorporating genetic improvement.

4.3 Bridging establishment and management: practical implications for birch silviculture

In my thesis I have presented findings from five studies addressing both the establishment and management of planted silver birch. However, from a management perspective, certain considerations must be acknowledged. The following section summarises key practical takeaways. In addition, although Scots pine and Norway spruce were not the species addressed in this thesis, a brief discussion of these species is included. This is because Scots pine and Norway spruce are the dominant reference species in Swedish forestry, with extensive knowledge available on their management. Comparing birch with these species helps to place birch in a broader silvicultural context, and highlights both similarities and key differences in management challenges and opportunities.

4.3.1 From planting to rotation: early decisions, site choice, and their long-term impacts

Silver birch typically thrives on fertile sites that offer adequate soil moisture (Niemistö *et al.* 2008; Hynynen *et al.* 2010). Dry microsites should be avoided for planting, especially in combination with mounding as shown by Nordin *et al.* (2023). Planting silver birch in drier spots may exacerbate drought stress and harm seedling performance. Naturally, this implies avoiding dry sites or sites prone to drought stress in general. Site fertility may also influence tree responses to cervid-induced browsing (Danell & Bergström 1989; Edenius *et al.* 1993; Persson *et al.* 2007). A combination of improved planting material and favourable site conditions may not only enhance the compensatory ability for birch under browsing but also promote growth, potentially allowing the saplings to escape browsing earlier. Poorer sites might have the opposite effect. More fertile sites offer higher growth potential. However, the enhanced growth will require earlier thinning interventions compared to less-productive sites, especially in denser settings (Rytter & and Werner 2007). On more fertile sites, which are typically rich in competing vegetation (Nilsson *et al.* 2010b), additional management efforts such as vegetation control through tending or MSP, may be required. Ultimately, the choice of initial spacing, in combination with site fertility, will influence the timing and frequency of subsequent management interventions while also having the potential to accelerate stand development and enable earlier harvesting.

4.3.2 Browsing mitigation in silver birch stands: silvicultural recommendations and societal trade-offs.

The challenge of protecting young forest stands, including silver birch, from browsing involves both silvicultural measures, such as site selection and plant protection, and societal dimensions, including landowner incentives, wildlife management, and solutions for stakeholder conflicts.

Birch planting decisions should be based on browsing risk assessments. In light to moderate browsing risk areas, planting silver birch with less intensive protection measures like repellents should be feasible. Selection and continuous focus on the selected crop trees may further enhance operational efficiency, both in terms of time and cost. This is particularly relevant given emerging repellent application advancements, such as application by drones, which may further streamline protection measures. Repellent application from drones remains tentative at this stage but represents a promising direction for future development. Alternatively, acoustic deterrents such as predator playbacks or portable ultrasound devices have shown promise in reducing browsing and crop damage (Laguna *et al.* 2022; Widén *et al.* 2022), though their long-term effectiveness remains uncertain. Ultimately, in high-risk areas with dense multi-ungulate populations, planting silver birch must be carefully considered. In such cases, fencing remains the most effective solution for the protection of young trees, although it is also expensive (Burņeviča *et al.* 2023). Erecting a fence may allow for certain flexibility in planting density, i.e., the initial density can be lower, as there is no need to account for the risk of browsing damage to the trees as long as the fence is intact and maintained. Planting strategies may also be adapted to landscape-level conditions. By contrast, these may be much more difficult to predict because of the complex relationship between the different cervid species, their habitat selection strategies the dispersion of forage in space and time (Zweifel-Schielly *et al.* 2012).

There is also a social dimension. Achieving a balance among the interests of various stakeholders has long been a major objective. However, reaching such a consensus has proven far easier said than done. This stems from the differing interests held by forest owners, hunters and the broader society, resulting in a longstanding conflict (Ezebilo *et al.* 2012; Loosen *et al.* 2021; Neumann *et al.* 2024). Maintaining high moose and deer populations, although preferred by hunters who want easily accessible game (Ball & Dahlgren 2002), will inevitably lead to forest damage and associated economic losses. Diverging views between hunters and forest owners may be further exacerbated by misperceptions of the true extent of browsing damage in young forest stands (Ezebilo *et al.* 2012). A potential solution lies in improving the accuracy and communication of data associated with forest damage, alongside with the development of updated and more effective local wildlife management strategies.

4.3.3 Integrating modelling tools into operational planning

Functions that model the development of genetically improved silver birch are essential for supporting long-term planning and decision-making in operational forestry. The models presented in Paper V, based on the two-parameter Korf function, offer a reliable framework for predicting basal area growth under different genetic improvement levels. Genetically improved material is expected to enhance production, increase economic returns, and reduce the optimal rotation age as shown by our simulations. However, as demonstrated in Section 4.2.3, the developed functions have certain limitations. Residual analysis showed a slight tendency for over-predicting basal area, particularly beyond 40 years, which means caution is needed for long-term projections. Paper IV showed different volume production between moderate and heavy thinning regimes. However, the model of Paper V cannot account for the impact of management, e.g., the effect of thinning regime applied, as the thinning component was not integrated into the modelling framework. Lastly, if mortality was not explicitly modelled, it can be accounted for using separate mortality functions. Overall, the new basal area model offers an important advancement in forecasting stand development while accounting for genetically improved material; however, its applicability under extreme or alternative management regimes remains limited, thus caution must be exercised. This highlights the need for individual-tree-level functions that could be incorporated into the decision support system Heureka, to account for genetic improvement effects and management scenarios such as varying thinning regimes.

4.3.4 Silvicultural contrasts between silver birch and conifers

Birch, including silver birch, is currently significantly less represented in the Swedish forest landscape than conifers. However, recent advancements in silver birch breeding have opened new possibilities for increasing its competitiveness. Compared to conifers, birch benefits from a shorter breeding cycle and earlier onset of flowering (Koski & Rousi 2005; Salojärvi *et al.* 2017; Fahlvik *et al.* 2021), often around ten years (Lepisto 1973), making genetic improvement more efficient. In addition, the much smaller genome of birch compared to conifers (Sharma *et al.* 2023), makes silver birch a promising candidate for genomic selection techniques. Its fast breeding cycle and relatively short rotation periods allow for genetic gains to be realised faster in practical forestry.

During the establishment stage, reducing pine weevil damage risk (Wallertz *et al.* 2014; Nordlander *et al.* 2017; López-Villamor *et al.* 2019; Domevscik *et al.* 2024) and competing field vegetation (Nilsson & Örlander 1999), mostly through MSP (Örlander 1996; Nilsson *et al.* 2010b; Löf *et al.* 2012), are major considerations for conifers. For silver birch, MSP is likely more beneficial for reducing competition from field vegetation (Karlsson 2002), as pine weevils generally do not feed on birch, although it has also been observed (Löf *et al.* 2004; Toivonen & Viiri 2006; Wallertz *et al.* 2014).

Spacing at planting can have long-term impacts on individual tree diameter of silver birch, as shown by Paper I. Similarly, research on spacing has consistently shown that diameter also increases with spacing in Norway spruce (Wiksten 1965; Gizachew *et al.* 2012) and Scots pine (Eklund 1956; Nilsson & Albrektson 1994; Malinauskas 2003). Conversely, narrower spacing or higher initial densities are likely to increase production. While tree quality mostly depends on whether the regeneration material is planted or naturally regenerated (Johansson 1997; Agestam *et al.* 1998), initial spacing can further contribute to quality of the trees. As shown by Liziniewicz (2014), narrow initial spacing generally yields higher-quality timber, providing both more opportunities for selecting the best crop trees and producing stems with smaller branches due to the increased competition compared to wider spacing (Agestam *et al.* 1998). However, as initial spacing decreases, the risk of declining vigour due to accelerated crown recession also increases (Harrington *et al.* 2009), which may be especially crucial for light-demanding species, such as birch, which recover and restore their crowns slowly (Bernadzki *et al.* 1980).

Later in stand development, browsing by cervids can be problematic for silver birch, especially in areas with dense cervid populations. Browsing also poses a major risk to Scots pine, which serves as an important food source for moose during the winter (Bergström & Hjeljord 1987; Nikula *et al.* 2004; Wallgren *et al.* 2014; Nilsson *et al.* 2016; Nikula *et al.* 2021). Browsing on Norway spruce may also occur (Bergquist & Örlander 1998; Bergquist *et al.* 2001; Bergquist *et al.* 2003a; Spitzer 2019), particularly under high deer densities or limited forage availability. However, due to its lower palatability to cervids (Cederlund *et al.* 1980; Shipley *et al.* 1998; Spitzer 2019) compared to silver birch and Scots pine, Norway spruce is less likely to be browsed making protective measures generally unnecessary. Conversely, Scots pine, similarly to silver birch, is likely to require either repellents or fencing as protective measures in cervid-rich areas. While Scots pine can also compensate for growth losses, cervid-induced damage is likely to harm its growth and stem quality (Edenius *et al.* 2002a; Wallgren *et al.* 2014; Matala *et al.* 2020), and economic returns (Nilsson *et al.* 2016). Moreover, owing to silver birch's faster growth and arguably better compensatory ability compared to Scots pine (Hester *et al.* 2004), its earlier escape from the browsing window may reduce the likelihood of sustained damage. However, an important distinction is that birch is also browsed during summer, unlike Scots pine which is primarily browsed in winter. This extended browsing period may limit the effectiveness of repellents, as shoots emerging during the summer become unprotected. Furthermore, the fact that conifers are evergreen may also influence the effectiveness and longevity of repellents, as their persistent foliage can retain protective substances differently compared to birch.

In silver birch, heavier thinning promotes individual tree growth at the cost of reduced total production as shown in Paper IV. Similarly, thinning effects in Norway spruce and Scots pine follow comparable trends (Mäkinen & Isomäki 2004a; Mäkinen & Isomäki 2004b; Nilsson *et al.* 2010a). Nilsson *et al.* (2010a) showed that heavy thinning substantially reduced gross volume production for both Scots pine and Norway spruce. Furthermore, heavy thinning significantly lowered merchantable timber volume in Scots pine as compared to an unthinned control, while none of the thinning treatments significantly raised merchantable timber volume. In Norway spruce, less-frequent heavy thinning and light thinning resulted in a significantly higher merchantable timber volume (Nilsson et al. 2010a). However, merchantable timber volume may also depend on earlier management interventions such as PCT (Huuskonen & Hynynen 2006). In silver birch, no significant differences in merchantable timber volume were found between heavy and moderate thinning regimes (Niemistö & Huuskonen 2025). Interestingly, the results of our study showed that dominant trees tend to grow faster than small trees, regardless of thinning treatment. This indicates that thinning regimes should be adapted to species. While Norway spruce may tolerate a range of thinning intensities, silver birch may benefit more from heavier thinnings, whereas Scots pine is likely best managed under a moderate thinning regime. Based on the self-thinning models for even-aged stands developed by Hynynen (1993), a mean diameter of 20 cm corresponds to approximately 1000 stems ha^{-1} for silver birch, 1250 for Scots pine, and 1800 for Norway spruce, indicating species-specific differences in stand dynamics and supporting the need for tailored thinning regimes. However, there may be a need to evaluate thinning strategies for silver birch that are more climate adapted, as has been done for Scots pine (de Castro Segtowich 2025).

5. Conclusions and future perspectives

Climate-change-induced risks underscore the need for change in Swedish forestry. As this thesis proposes, introducing more birch could be one way to diversify the currently conifer-dominated forest landscape. Using genetically improved planting material offers birch with better vitality, growth and quality – making it a viable option in production forestry.

Establishment: Successful establishment of silver birch requires careful consideration of initial spacing and browsing risk. Narrower spacing may help distribute browsing pressure and promote higher-quality stems but may increase competition and mortality if not managed properly. On the other hand, wider spacing supports faster individual tree growth but may concentrate browsing on fewer stems. As our results suggest, silver birch remains vulnerable to damage, especially in high-cervid-density areas where the need for protective measures is considerable. However, in areas with low-to-moderate browsing risk, silver birch's fast growth and compensatory ability may reduce the need for intensive protection as trees can escape the browsing window relatively quickly.

Management: Silvicultural management of silver birch entails a trade-off between maximising volume growth and producing large-diameter, high-quality timber. In this thesis, heavier thinning enhanced individual tree diameter growth, although it came at the cost of total volume production. Thinning responses in silver birch suggested that dominant trees benefit the most from thinning interventions, implying that early identification and targeted management of future crop trees may be the most effective silvicultural strategy when aiming for high-quality timber production.

However, site conditions and management objectives must guide decisions, which must in turn be supported by up-to-date growth functions adapted to improved material. As shown by the new basal area functions developed in this thesis, rotation lengths and economic outcomes can shift significantly when accounting for genetic improvement.

Future perspectives: As interest in planted birch continues to grow, future research should focus on the key uncertainties that remain, particularly concerning establishment success under browsing pressure and how this interacts with initial stand density. Future research should prioritise understanding these dynamics, including the potential for using denser birch stands or mixtures to mitigate damage. The role of PCT as a management tool also warrants further investigation. From a climate adaptation perspective, thinning regimes should be validated across site types and under future climate scenarios to ensure resilience and long-term productivity. Lastly, there is a pressing need for updated growth functions incorporating genetic improvement effects that are compatible with decision support systems such as Heureka. This will enable dynamic modelling of forest trees and stands under various management regimes.

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Popular science summary

Silver and downy birch form the third-most-common tree species group in Sweden, accounting for twelve percent of total growing stock. Once considered to be undesirable species in conifer-dominated stands, birches have gradually gained interest among forest owners. This is largely due to advances in birch breeding and the resulting genetically improved planting material which offers better vitality, quality and growth. In some Baltic Sea countries, such as Latvia and Finland, birch has held a more prominent role in forestry, often being cultivated not only as pulpwood, but also high-quality timber used in plywood production. Furthermore, birch can also promote biodiversity, and it grows well in mixtures with other tree species, such as Norway spruce.

This thesis explored how planted silver birch can be established and managed more efficiently. It addresses key questions such as choice of density, damage caused by browsing animals like moose and deer, and the effects of different thinning strategies. Regarding establishment, the results showed that wider spacing or fewer trees per hectare can be useful for promoting individual tree diameter growth. On the other hand, narrower spacing or more trees per ha can promote total production. Regarding browsing by deer and moose, light-to-moderate browsing showed limited impact on the survival and growth of birch seedlings owing to birches' resilience to damage. However, as shown by our surveys, under high browsing risk, tree survival and growth can be affected strongly. In such cases, protective measures should be used. Regarding management, the results showed that heavier thinning and a focus on dominant trees from the beginning can help produce high-quality timber more efficiently. Furthermore, as shown by our models, using genetically improved material and proper management can

improve not only growth, but also reduce rotation length and increase overall profit.

In conclusion, forest owners should plant enough seedlings to both meet their management goals and account for the local browsing risk. Protective measures may be necessary, especially in areas with a lot of moose and deer. Management-wise, if the goal is large-diameter high-quality timber, use planting in combination with heavy thinning; otherwise, higher total volume production may be achieved by more moderate thinnings.

Populärvetenskaplig sammanfattning

Vårt- och glasbjörk utgör tillsammans tolv procent av den totala stående volymen i Sverige. Bara gran och tall har ett högre virkesförråd. Tidigare ansågs inte björken som ett önskvärt inslag i produktionsskogen, men på senare tid har intresset för trädslaget ökat. Det ökade intresset beror till viss del på de framsteg som har gjorts i förädlingsarbetet med vårtbjörk och som har resulterat i material med bättre vitalitet, kvalitet och tillväxt. I Lettland och Finland har björk länge varit en viktig del av skogsproduktionen och har inte bara använts för massaved utan också som timmer och plywood. Björk kan också bidra till att öka biodiversiteten och kan användas i blandning med andra trädslag som exempelvis gran.

Denna avhandling undersöker hur planterad vårtbjörk kan föryngras och skötas mer effektivt. Forskningsfrågor som studerats är val av förband vid plantering, betesskador av älg, rådjur och hjort, och effekter av olika gallringsstrategier. Resultaten visade att plantor planterade i glesa förband, dvs färre planterade plantor per hektar, kan vara ett sätt att öka diametertillväxten för enskilda träd. Å andra sidan visade resultaten att många plantor per hektar i täta förband ökade den totala volymproduktionen per hektar. Lätta till måttliga betesskador av älg och hjort hade begränsad effekt på överlevnad och tillväxt hos vårtbjörk. Detta på grund av trädslagets snabba ungdomstillväxt och förmåga till kompensatorisk tillväxt. Vid högt betestryck kan dock överlevnad och tillväxt påverkas betydligt och åtgärder måste då vidtas för att skydda plantorna mot bete. Resultat från gallringsstudierna visade att hårda gallringar för att gynna tillväxt hos dominanta träd med bra kvalitet kan bidra till en effektiv produktion av timmer av hög kvalitet. De tillväxtmodeller som gjordes visade att användning av genetiskt förädlat material och effektiv skötsel inte bara påverkade tillväxten utan kan också korta omloppstiderna och bidra till en väsentligt förbättrad ekonomi.

Slutsatser från studierna var bland annat att skogsägare bör plantera tillräckligt många plantor för att möta målen med deras skogsskötsel, men också för att kompensera för låga till måttliga betesskador. I områden med högt betestryck kan olika skydd mot bete vara nödvändigt. En annan slutsats var att om slutmålet är grova träd av god kvalitet så kan plantering i kombination med hårda gallringar rekommenderas. Om målet istället är hög virkesproduktion bör ett gallringsprogram med relativt svaga gallringar användas.

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Andis

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III

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Effects of simulated browsing on survival, growth, and stem quality of silver birch

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ABSTRACT
Cervids significantly challenge the establishment of planted silver birch (*Betula pendula* Roth.) as browsing impacts tree growth, morphology, and stem structure, impacting wood quality and increasing probability of mortality. This study aimed to evaluate the effects of cervid damage on silver birch by simulating browsing of different timing, duration, and intensity in a randomized block experiment established in southern Sweden. The treatments represented winter and summer browsing for timing, repeated applications for duration, and varying levels of biomass removal for intensity. After three growing seasons, survival rates were high (89.6–95.6%) with no significant differences among treatments. Mean annual height growth and ground-level diameter growth were 69.01 cm yr^{-1} and 9.94 mm yr^{-1}, respectively. The effects of the simulated browsing treatments on growth outcomes were small and not statistically significant, however, the effect on quality was significant. Silver birch is likely to withstand light to moderate browsing due to compensatory growth. Higher browsing intensity increases the risk of lower-quality stems, potentially reducing the commercial timber quality of future merchantable trees. These results highlight the necessity of targeted management strategies to reduce quality losses in birch regeneration efforts under browsing pressure.

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Betula pendula; herbivory simulation; cervids; early growth; survival

Introduction

Forests, both globally and in Sweden, provide a variety of ecosystem services and commodities, among which timber can be regarded as the most valuable product (KSLA 2024). As in the rest of Northern and Eastern Europe, conifers such Norway spruce and Scots pine dominate the forest landscape, with *Betula spp.* usually being the most abundant broadleaf tree. Generally, in Northern and Eastern Europe, silver birch (*Betula pendula* Roth.) is one of the most important species for veneer production. In Sweden, the value of and interest in birch wood use have grown noticeably in recent years (Lidman et al. 2024), driven partly by advancements in tree breeding (Liziniewicz et al. 2022), and the increasing need for more diversified forests and forestry practices (Bakx et al. 2024; Felton et al. 2024). Concurrently, certain tree species including *Betula spp.* constitute a substantial part of a diet of cervid species (Rea 2011; Pfeffer et al. 2021; Kullberg and Bergström 2001; Månsson et al. 2007; Bergqvist et al. 2014). The main browsers in Swedish forests include moose (*Alces alces*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and red deer (*Cervus elaphus*) (Viltdata 2022). The abundance of cervids in the Swedish forest landscape has emerged as one of the most significant challenges for young trees in their establishment phase (Nilsson et al. 2010; Ara et al. 2022).

Growth responses of trees to herbivory and the exact mechanisms by which trees cope with damage are complex and not well-studied (Persson et al. 2005). Tree growth responses to browsing are partly explained by the degree and characteristics of the inflicted damage, e.g. number of damaged shoots, position of the damage as well as timing and frequency. The type and characteristics of damage may depend on the specific cervid species and their foraging patterns, which vary seasonally and spatially (Månsson et al. 2007; Zweifel-Schielly et al. 2012). Seasonal changes in the life cycles of broadleaved trees influence cervid diets, typically increasing the consumption of green biomass during the active growing season (Persson et al. 2000). When trees are dormant, cervids eat only woody biomass, however, different species consume different amounts of total biomass (Kullberg and Bergström 2001). While removal of leaf area during the active growing season may directly affect the total carbon assimilation of a tree, winter shoot browsing affects trees' subsequent growing season, resulting in

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potentially different tree growth responses (den Herder et al. 2009).

Research has demonstrated that browsing can affect stem morphology and tree growth (Bergstrom and Danell 1987; Persson et al. 2005). In the worst case, severe damage may kill trees (Lyly et al. 2014; Wallgren et al. 2014). The influence of browsing on birch species have been assessed in studies investigating various response variables like leaf and shoot biomass (Bergström and Danell 1995), morphology and biomass (Bergstrom and Danell 1987) and bud development (Danell et al. 1985). All studies have shown the negligible or nonexistent effect of browsing on the survival of silver birch (e.g. Bergström and Danell 1995; Bergstrom and Danell 1987). Additionally, birch has demonstrated a capacity for compensatory growth (Hjálten et al. 1993), meaning it can replace lost tissues by producing new shoots and leaves after damage, thereby maintaining overall growth despite browsing. However, these studies primarily focused on naturally regenerated birch, leaving uncertainty about how planted silver birch responds under controlled conditions.

Little to no attention has been given to the combined effects of browsing severity, timing, and duration on stem quality traits, particularly in relation to future timber quality. For silver birch, ensuring high stem quality is more important for veneer production than for the production of pulpwood (Luostarinen and Verkasalo 2000; Niemistö et al. 2008). Cervid-induced stem defects may result in external quality defects, such as forks, bends, and spike knots. They can also lead to more severe internal issues like discoloration and decay (Härkönen et al. 2009; Rea 2011) that are highly undesirable for veneer production (Luostarinen and Verkasalo 2000). However, certain imperfections may still be tolerated in plywood manufacturing, depending on grading criteria and end-use standards. Given the lack of research, more comprehensive studies focusing on both growth and quality traits in planted birch stands hold not only a clear scientific value but also great practical relevance for forestry.

This study aimed to investigate the effect of simulated browsing on initial growth responses of planted silver birch. The following hypotheses were adopted: (H1) Survival and growth are negatively correlated with browsing duration and intensity. (H2) Survival and growth are negatively affected by browsing on leading shoots, while browsing on side shoots or leaf removal does not have a significant impact. (H3) Browsing on leading shoots significantly increases the number and severity of stem quality defects like spike knots and double tops whereas browsing on side shoots or leaf stripping does not exacerbate quality issues.

Material and methods

Study area & experimental design

The study site was located in Fulltofta, municipality of Hörby, Skåne county in southern Sweden (55.8825° N 13.6550° E; Figure 1(a)). The experiment was established in May 2021 on a fertile site with site index G40 (indicating a height of 40 m of the dominant Norway spruce (*Picea abies* L. Karst) trees at a reference age of 100 years (Hägglund and Lundmark 1977)). The previous stand was a Norway spruce monoculture which was clear-felled in the winter of 2020. Prior to the installation of the experiment, mechanical site preparation by patch scarification was done. In addition, a fence was installed around the area to prevent damage from cervids and to minimize disturbance from human activity. Slightly under 1,000 silver birch seedlings were planted, all originating from the Ekebo 5 seed orchard (Figure 1(a)) – a third-generation greenhouse seed orchard located in southern Sweden (south of 60°N), established to produce material adapted to this region (Fahlvik et al. 2021). Seedlings were grown under standard nursery conditions and were two years old at planting – spending one season in plug trays followed by one year in transplant beds. As the material was derived from a single, standardized seed source, variation due to differences in genetic origin was minimized. Within each block, twelve browsing treatments were randomly assigned to the planted seedlings and two were left as untreated controls, resulting in a total of 13 different treatments studied in a randomized block design with a total of 71 blocks (Figure 1(b)). The scarified patches were not evenly distributed and varied in their size, but in most cases the spacing between the seedlings was 1–1.5 m.

Based on the seasonal foraging characteristics of the different cervid species, treatments were divided into two main classes depending on the season (Figure 2): (1) Clipping of shoots during winter (December–January) and (2) stripping leaves during summer (June–July). Clipping was carried out in three different ways: (1) TS – clipping of a top shoot of a seedling, (2) SS – clipping of 50% of side shoots of a seedling and (3) TSSS – clipping of top shoot and 50% of side shoots of a seedling. Summer stripping subclasses were: (1) LLS – light leaf stripping, i.e. around one third of leaves would be stripped and (2) MLS – moderate leaf stripping – around two thirds of leaves of a tree would be stripped. In addition, a pair of extra heavy treatments were added to the treatments. The extra heavy (EH) treatment combined the heaviest winter browsing (WB) and summer browsing (SB) treatments, i.e. TSSS and MLS. All treatments were further

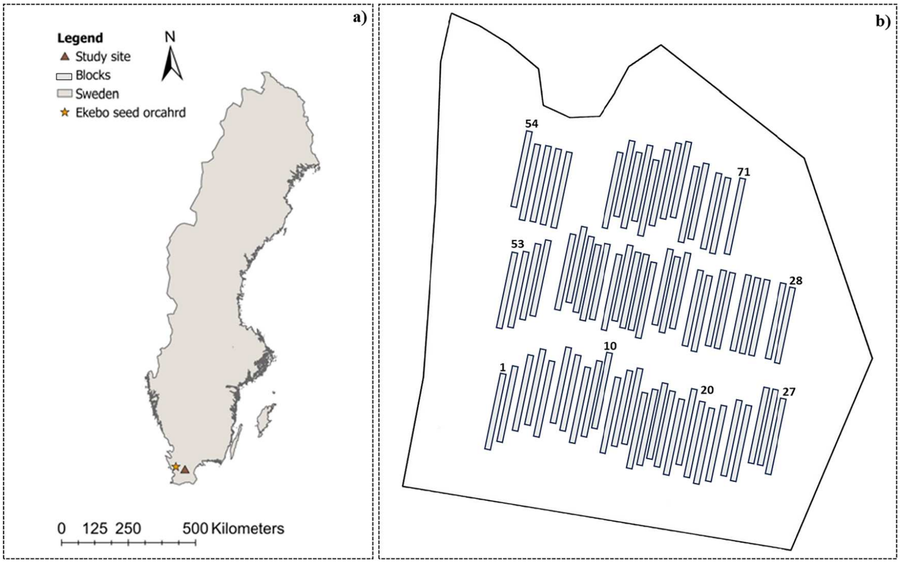

Figure 1. The (a) depicts study location and location of the seed orchard within Sweden and (b) experimental layout. In (b) each block consists of 14 seedlings with the randomly assigned treatments.

subdivided into versions with one or two years duration over the period of 2021–2022. Lastly, a control treatment (no stripping or clipping applied) was also included in the experimental design.

Treatments, data collection and processing

The summer treatments (stripping leaves) were done by stripping leaves off the selected branches, whereas winter treatments (clipping shoots) were done by clipping the selected shoot(s) using gardening clippers. To mimic real-life conditions as closely as possible, the maximum shoot size (diameter) of the clipped shoots was adopted from the modeled diameter sizes specifically for moose and birch (Shipley et al. 1999). To minimize disturbance to the long-term experiment and for logistical reasons, seven seedlings from two blocks were destructively harvested during each treatment period from summer 2021 to winter 2022. This resulted in a total of 28 seedlings being completely harvested over the two-year period. These samples were used to estimate the total removed and remaining biomass, helping to illustrate the relative severity of each treatment.

Seedling mortality, height and ground-level diameter were recorded over a three-year period and quality traits (such as apical dominance and occurrence of quality issues due to damage) were recorded during the last inventory. The first inventory was conducted in 2021, right after planting, to measure the starting conditions. Subsequent inventories were carried out in the winters of 2022 and 2023 to assess the effects of the treatment. Height was measured with a precision of 0.1 m.

The removed mean biomass was measured during both the summer and winter inventories in 2021 and 2022 as visualized in Figure 3. Ground-level diameter was measured using digital calipers to the nearest 0.01 mm. All the removed leaf and stem biomass was collected on site, placed in paper bags and transported to a laboratory where they were left to dry at room temperature for about one week. Thereafter, all of the samples were placed in a drying oven (*Termaks, Series TS9000*) for two days at 100°C or until reaching a stable weight. Following drying, all samples were weighed using an electronic scale (*OHAUS PX Series Balance*) to a precision of 0.001 g.

Assessment of quality traits

During the final assessment in 2024, the quality of all remaining trees was evaluated. The quality was assessed according to a pre-defined set of four quality classes: (a) trees with no visible stem defects, (b) trees with a bent stem exhibiting any degree of curvature, possibly accompanied by a secondary stem that is < 50% of the basal diameter of the main stem, (c) trees with spike

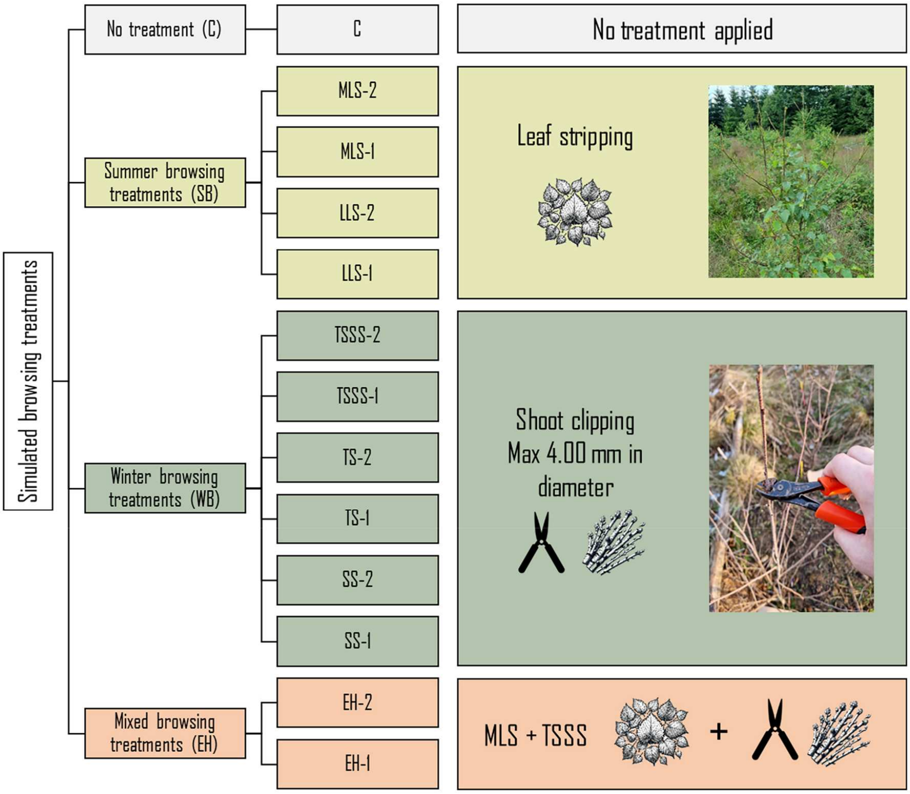

Figure 2. Treatments tested in this study: LLS – light leaf stripping, MLS – moderate leaf stripping, TSSS – clipping of top shoot and side shoots, TS – clipping of top shoot, SS – clipping of side shoots, EH – extra heavy treatment – combining both TSSS and MLS treatments. The numbers 1 and 2 indicate the number of years the treatments are applied.

knots (branches angled at ≤ 30° from the main stem that are < 50% of the basal diameter of the main stem), and (d) trees with forks (one or more additional living stem ≥ 50% of the basal diameter of the main stem and roughly of the same height; Figure 4). In addition, the height at which each issue occurred was recorded. In case of multiple stems present, the diameters of the stems at the height at which the issue occurred were recorded.

During data preparation for the analysis, trees were categorized into two groups: those with quality issues such as bends, spike knots, or forks (b – d) and those without any quality issues (a).

Statistical analysis

All data computations and analyses were carried out in R (version 4.3.2; R Core Team 2024). By default, a significance level $\alpha < 0.05$ was used for testing the null hypotheses of no difference between the treatments. The model structure was determined a priori in accordance with the experimental design, expected treatment effects, and the nature of the response variables.

Mortality after three growing seasons was evaluated using a generalized linear mixed model (GLMM). The model was fitted using the R package *glmmTMB* (Brooks et al. 2017). To account for the binary nature of the mortality data (i.e. 1 = alive, 0 = dead) we employed a GLMM of binomial family using a logit link. The mathematical formula of the specified model was:

$$log\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = \beta_0 + \beta_1 treat_{ij} + block_j, \quad (1)$$

where π_{ij} is the probability of the outcome for sapling vitality for treatment *i* in block *j*, β_0 is the intercept representing the baseline outcome at the reference level, β_1 is the coefficient for the treatment effect, $treat_{ij}$ is the fixed

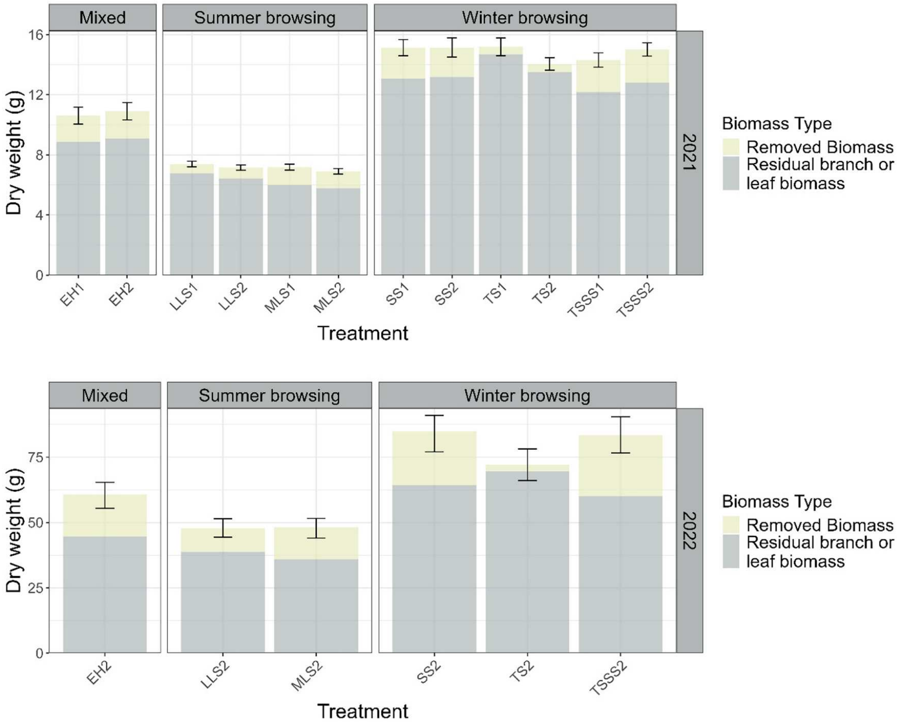

Figure 3. Dry weight of mean total biomass removed in 2021 and 2022. The upper panels show data from treatments applied during the 2021 growing season, while the lower panels show data from treatments applied in 2022. Residual branch or leaf biomass was estimated for all remaining seedlings (n = 67-69 in 2021 and n = 62-67 in 2022) using destructively sampled seedlings (n = 14 per year, in 2021 and 2022). Measured biomass removal was based on seedlings per treatment with valid measurements (n = 67-69 in 2021 and n = 62-67 in 2022). The different facets within each panel represent the respective treatment groups. Error bars indicate standard errors. Removed biomass was measured, whereas total branch and leaf biomass has been estimated via multiple linear regression (Eq. 4), based on an average of seven destructively sampled seedlings per inventory. The total branch biomass indicates the remaining (standing) mean biomass per treatment. The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped), TSSS (both top and side shoots clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied).

effect of i^{th} treatment and j^{th} block, $block_j$ is the random effect of the j^{th} block.

Sapling height (H) and ground level diameter (GLD) after three growing seasons were evaluated using a linear mixed model (LMM). The model (Eq. 2) was fit using package *glmmTMB* in R (Brooks et al. 2017). Given the continuous nature of variables H and GLD, we employed LMMs of Gaussian family and identity link function. The error term is assumed to be normally distributed, which was observed in the model evaluation. The mathematical formula of the specified model for growth traits was:

$$Y_{ij} = \beta_0 + \beta_1 treat_{ij} + block_j + \varepsilon_{ij}$$
$$\varepsilon_{ij} \sim N(0, \sigma^2) \qquad (2)$$

where Y_{ij} is the measured H or GLD for the i^{th} treatment and j^{th} block, β_0 is the intercept, representing the mean height at the reference level, β_1 is the coefficient for the treatment effect, indicating the expected change in H associated with the treatment, $treat_{ij}$ is the fixed effect of i^{th} treatment and j^{th} block, $block_j$ is the random effect of the j^{th} block, and ε_{ij} is the random error for the combination of treatment i and block j. For both Eq. 1 and Eq. 2, model assumptions were evaluated via visual inspection of residual plots using the *DHARMa* package in R.

The occurrence of the different quality classes or issues (bends, spike knots, forks) was tested using a logistic regression model owing to its suitability for modeling binary outcomes. The model was fit separately

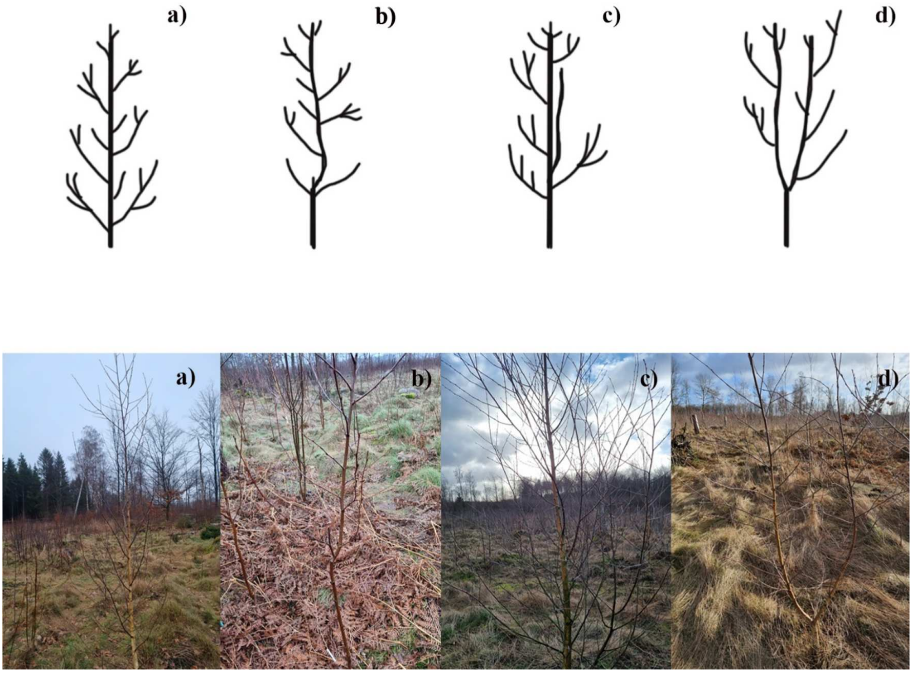

Figure 4. Example of the major quality classes observed in the trial, including: (a) no quality issues (straight stems and proportional crowns); (b) bends; (c) spike knots and (d) forks.

for every quality issue using the *glmmTMB* package in R with a binomial family and a logit link function. The model was specified as follows:

$$log\left(\frac{\pi_i}{1-\pi_i}\right) = \beta_0 + \beta_1 \times treat_i + \beta_2 \times height_i, \quad (3)$$

where π_i represents the probability of observing the binary outcome (e.g. present = 1, absent = 0) for observation *i*. The expression $log\left(\frac{\pi_i}{1-\pi_i}\right)$ is the log-odds of the outcome. β_1 and β_2 are coefficients for predictor variables treatment and height respectively. No explicit residual error term ε_{ij} is included, as variability in the response is modeled through the binomial distribution.

The samples collected through destructive sampling were used to fit models estimating total branch biomass and total leaf biomass. The following model was constructed:

$$Y_i = \beta_0 + \beta_1 height_i + \beta_2 diameter_i + \beta_3 (height_i \times diameter_i) + \varepsilon_i, \varepsilon_i N(0, \sigma^2) \quad (4)$$

where Y_i is dependent variable for i^{th} tree, representing the dry biomass of clipped shoots and stripped leaves respectively, β_0 is the intercept representing the predicted mean biomass at the reference level, β_1, β_2 and β_3 are the coefficients for height, diameter and the interaction term, indicating the expected change in biomass associated with the respective coefficients $height_i$, $diameter_i$ and $height_i \times diameter_i$, which are the independent variables of the i^{th} tree, and ε_{ij} is the random error for tree *i*.

Models were thereafter used to estimate the total branch biomass and total leaf biomass of all trees measured during the respective inventory.

Results

Survival

Following three growing seasons, seedling survival was high across all treatments (Figure 5), and there was no statistically significant difference in mortality between treatments (Appendix B). Out of 994 planted seedlings, six seedlings had died before July 2021 (second inventory, first growing season). Over the second and third growing seasons, 68 more seedlings died. In addition, 28 seedlings were removed by destructive sampling. Overall survival across treatments was 92.7% (Figure 5).

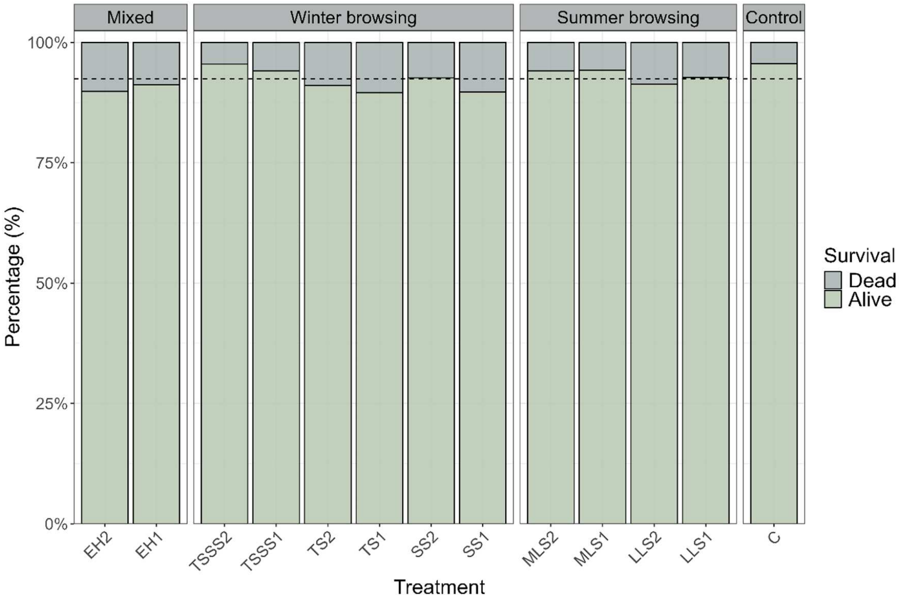

Figure 5. Registered mean seedling survival across the tested treatments. The different bars indicate different treatment groups. Percentages are based on the number of surviving seedlings per treatment. Sample size per treatment group ranged from n = 60-65 (n_{total} = 71); control group: n = 131 (n_{total} = 142). The groups and treatments within the groups are organized according to the assumed spectrum of severity from most severe (EH2) to least severe (C). The dashed line indicates average survival across all treatments. The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied).

Growth traits

Average height at the end of the third growing season varied between 230 and 260 cm for the treatments (Figure 6), but the differences were not statistically significant (Appendix B). During the first three growing seasons after planting, annual height growth was on average 69.0 cm year^{-1}. Average annual growth of ground-level diameter (GLD), varied between 9.4-10.4 mm year^{-1} between the treatments (Figure 7), and the differences were not statistically significant (Appendix B).

Quality traits

Individual tree analyses revealed different quality trait outcomes among treatments. The treatments did not affect the occurrence of forks and spikes, nor were any differences in branch diameter observed among treatments for any of the stem defect types (Appendix A). The most common quality issue was stem bends. Forks had an almost twice as high occurrence as spikes, which were the least common issue (Figure 8). For bends, treatments EH1, EH2, TS2, TSSS2, TSSS1 and TS1 were found to have a significantly higher occurrence compared to other treatments (Figure 8; Appendix B).

Treatments categorized under higher-intensity browsing, like top shoot clipping and especially repeatedly clipped, had a higher proportion of trees with 3–5 quality issues per tree than lower-intensity treatments (Figure 9). Summer browsing had a negligible proportion of trees with more than two quality issues; most trees had one or no quality issues, similar to the control treatment.

Discussion

Contrary to our initial hypothesis, survival and growth did not show significant negative correlations with browsing duration and intensity (H1), nor did browsing on leading shoots significantly reduce survival and growth (H2). Silver birch experienced high survival during the first three growing seasons in this study for all treatments. This finding aligns with earlier studies in Sweden. Bergstrom and Danell (1987) reported a survival rate of 100% for silver birch, irrespective of the browsing intensity applied. Similarly, no mortality was found in an

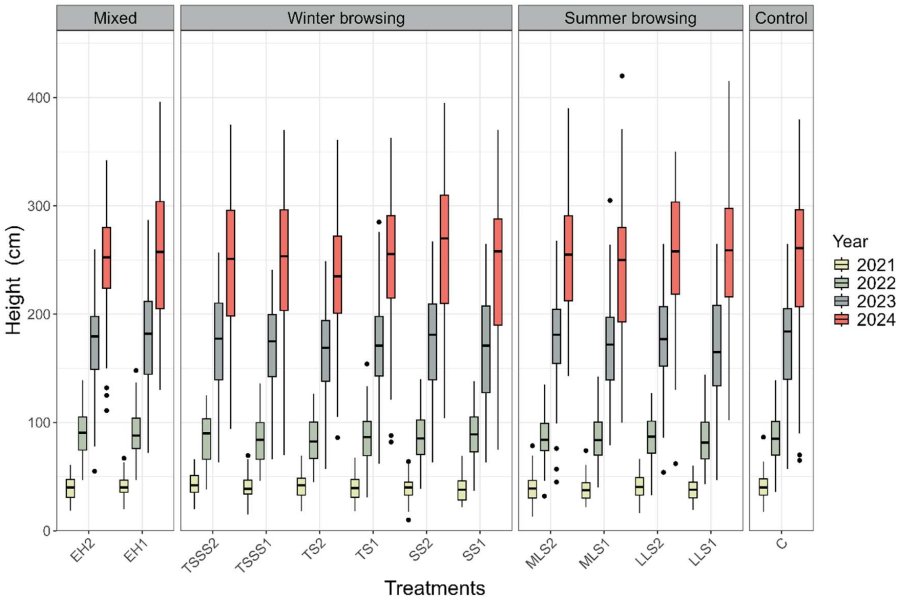

Figure 6. Measured mean height of the seedlings planted in Fulltofta across various treatments from 2021 to 2024. Each set of bars indicates a different treatment group. Sample size per treatment per year: n = 60–71; control: n = 131–141. The groups and treatments within the groups are organized according to an assumed spectrum of severity from most severe (EH2) to least severe (C). The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied). Boxplots display the median (central line), interquartile range (IQR; the box spans the 25th to 75th percentile), and whiskers extending to the most extreme values within 1.5 × IQR. Points beyond this range represent outliers.

earlier study simulating a range of summer browsing treatments (Bergström and Danell 1995). More recent studies also indicate negligible or no mortality (Persson et al. 2005, 2007). However, when exposed to natural browsing, survival of silver birch was found to be significantly lower in treatments exposed to the longest browsing pressure, i.e. up to 42 months (Bergquist et al. 2009). Additionally, the same study that reported no mortality for silver birch found 100% mortality of downy birch under the most severe browsing intensity (Bergstrom and Danell 1987), potentially indicating compensatory capacity differences between the two birch species.

The different browsing treatments tested did not significantly affect height or GLD. Similarly, Bergstrom and Danell (1987) found no height differences in silver or downy birch under light – to medium-intensity browsing. However, both species were significantly shorter under high browsing intensity compared to lower – and medium-intensity treatments. Analogously, Bergquist et al. (2009) found that prolonged exposure to browsing reduced height increment in silver birch, with the greatest reduction observed after at least three years of natural browsing. However, differences in provenance and growth phenology across studies may influence absolute outcomes, as growth responses are known to vary with genetic origin. Both browsing duration and intensity have been identified as significant factors influencing tree growth and morphology in previous studies, not only for birch (Persson et al. 2005) but also for Scots pine (Edenius et al. 1995; Wallgren et al. 2014). One possible explanation for these contrasting results could be this study's absence of higher-intensity and longer-duration treatments.

In line with H3, browsing on leading shoots caused significantly more stem defects such as bends. The increased occurrence of bends was particularly evident in treatments where the treetops were removed. Bends account for most of the increased number of quality defects on clipped trees. Single and multiple bends were most common in treatments removing the tree's apical leader. Changes in tree morphology, e.g. deformed stems, are likely a symptom of shoot apex damage or removal (Barbier et al. 2017). One of the few studies assessing the effect of browsing on birch quality (Rea 2011) showed a noticeable impact of

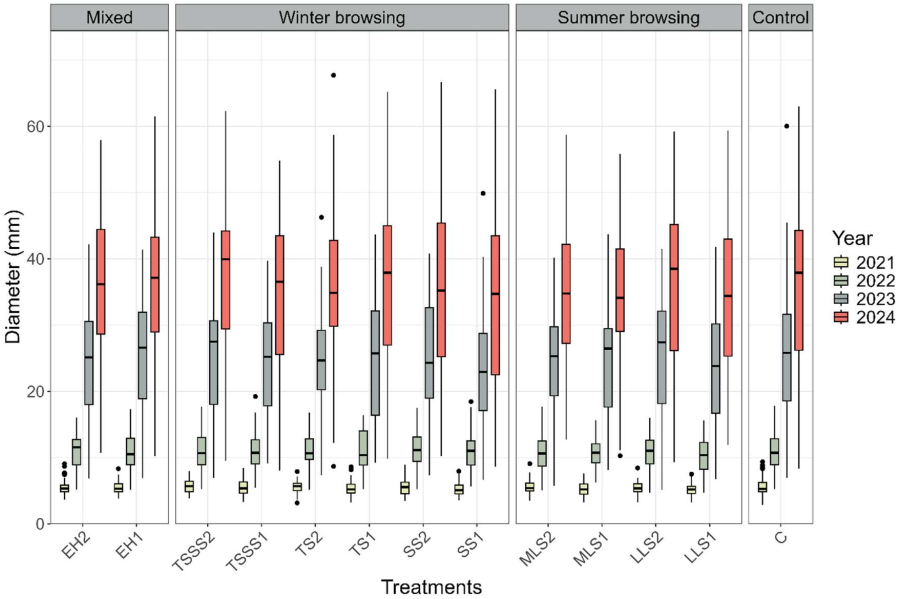

Figure 7. Measured mean ground-level diameter (GLD) of the seedlings across various treatments from 2021 to 2024. Each set of bars indicates a different treatment group. Sample size per treatment per year: n = 60-71; control: n = 131–141. The groups and treatments within the groups are organized according to an assumed spectrum of severity, i.e. from most severe (EH2) to least severe (C). The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied). Boxplots display the median (central line), interquartile range (IQR; the box spans the 25th to 75th percentile), and whiskers extending to the most extreme values within 1.5 × IQR. Points beyond this range represent outliers.

natural moose browsing on quality of paper birch (*Betula papyrifera*). Repeatedly browsed trees tended to develop quality defects both externally (crooks, multi-stems, bushy form, hedged-like crown structures) and internally (increased discoloration and decay caused by breakage of branches; [Rea 2011]). Bergquist et al. (2009), on the other hand, observed no significant changes in tree quality for silver birch browsed under natural conditions, whereas the quality of Scots pine was significantly affected. In Scots pine, severe top browsing increased the occurrence of stem deformations such as crooks (Matala et al. 2020). Matala et al. (2020) also reported a significant effect of high intensity browsing on occurrence of vertical branches, a quality defect similar to spike knots. However, even for Scots pine, the results vary across studies, potentially indicating not only differences between the species, but also potential interactions with environmental conditions (Wallgren et al. 2014).

As this study suggests, light to moderate browsing may not significantly reduce early growth or impair individual tree vitality. In such areas, targeted but less intensive protection measures like repellents which may deter browsing through scent and taste can help mitigate risks to survival and quality of the trees. Alternatively, measures such as freeze tape, a type of protective wrapping for seedlings and larger trees can also help to mitigate the damage, especially on leading shoots. Freeze tape shields young stems and shoots from direct damage and may discourage browsing to some extent. Selecting a combination of these methods based on site-specific browsing pressure, accessibility, and budget can reduce browsing damage in challenging areas.

Where multiple deer species have dense populations, high-intensity browsing risk increases and birch planting has to be carefully considered. In such environments, planting birch without any proper measures may be unwise. Fencing may remain one of the most effective browsing mitigation solutions, as it physically prevents ungulates from accessing young seedlings. However, fencing is costly due to high establishment and maintenance costs. Alternatively, temporary fences as described in (Bergquist et al. 2009) could be an option, as they can be reused at other regeneration sites, reducing the overall cost. Regardless, the strategy chosen must be

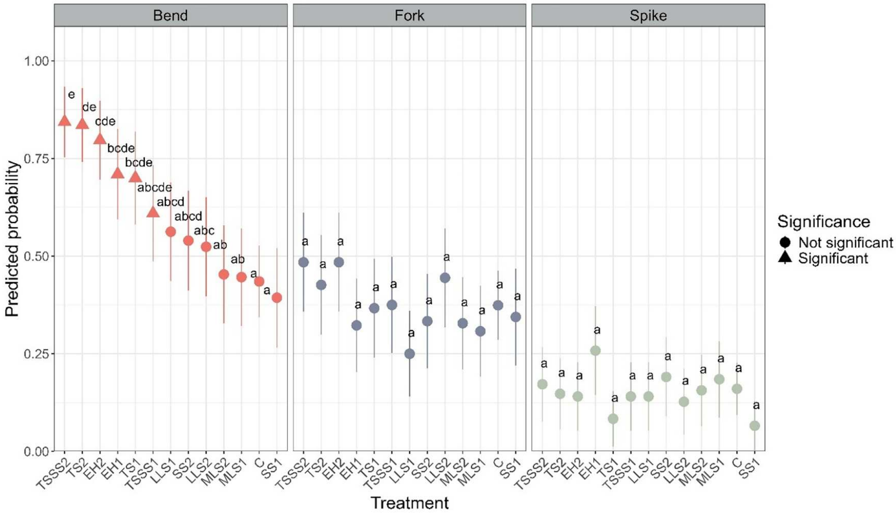

Figure 8. Modeled predicted probabilities extracted from the model (Eq. 3) and analyzed for significance by pairwise comparisons, accounting for multiple comparisons using a Sidak adjustment. Treatments within each quality issue sharing the same small letter are not significantly different from each other. The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied). Error bars represent 95% confidence intervals, and letters denote significant differences between treatments within each quality issue based on Eq. 3 and the subsequent post hoc tests.

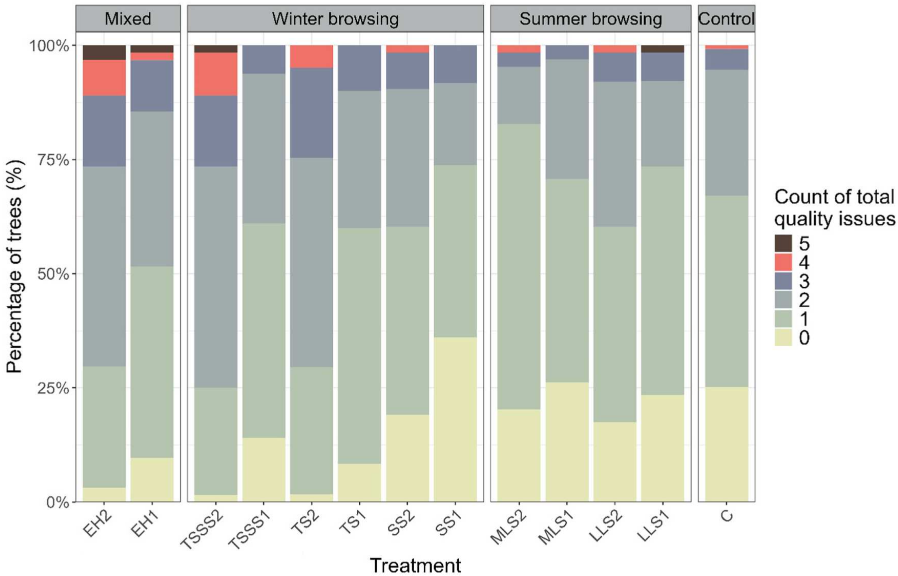

Figure 9. The percentage of trees displaying different total numbers of assessed quality issues. The different bars indicate different treatment groups. Quality assessment is based on surviving seedlings per treatment: n = 60–65; control = 131. The groups and treatments within the groups are organized according to an assumed spectrum of severity, i.e. from most severe (EH2) to least severe (C). The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied).

carefully considered based on the specific conditions of the site, the intensity of browsing pressure, and the long-term management objectives.

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Disclosure statement

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

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Appendixes

Appendix A. Branch diameter by quality issue and treatment type

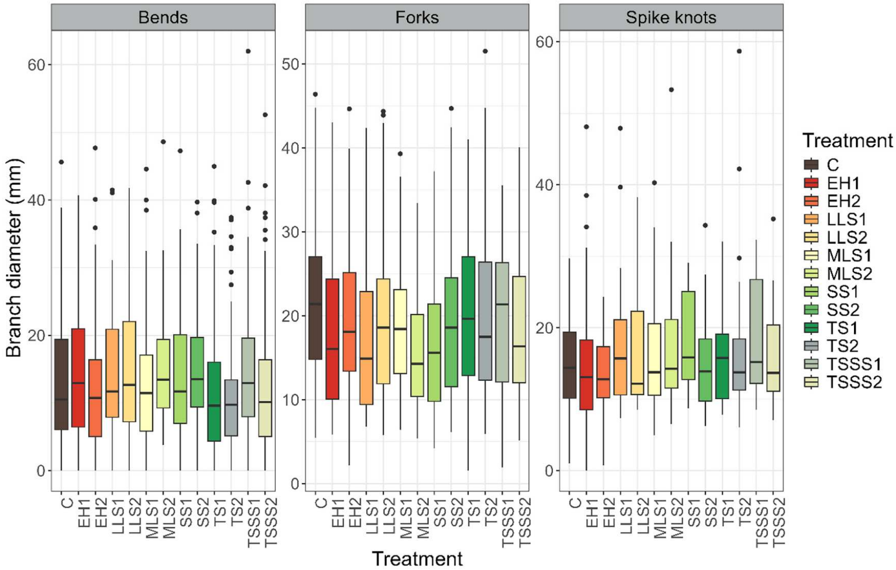


Figure A1. Measured branch diameters resulting from different quality issues, measured at the height of occurrence on the stem. Branch size assessment is based on surviving seedlings per treatment: n = 60–65; control = 131. Colors indicate different treatments. Each panel depicts a different quality issue observed on the trees: forks, bends and spike knots. The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped) and TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping), EH (an extra-heavy treatment combining MLS and TSSS), and C (control with no treatment applied).

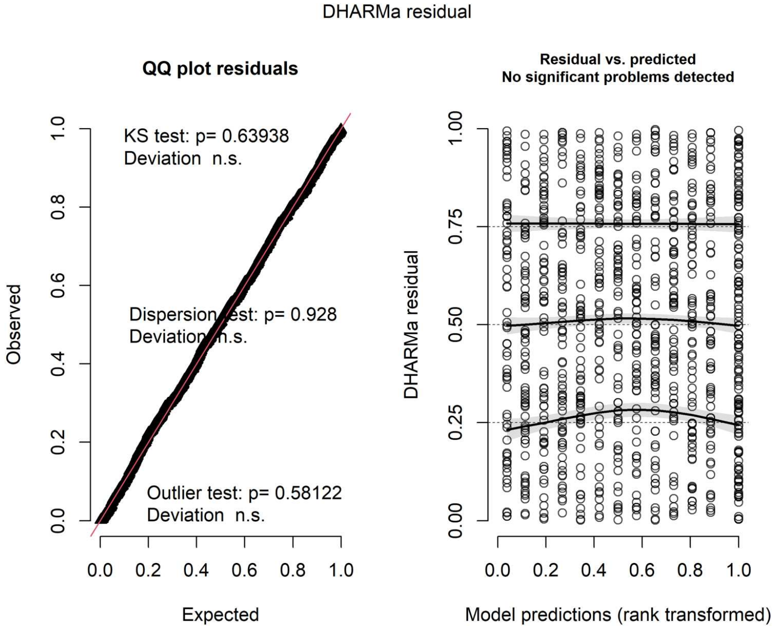
Appendix B

Table B1. Statistical outputs from the models run in this study.

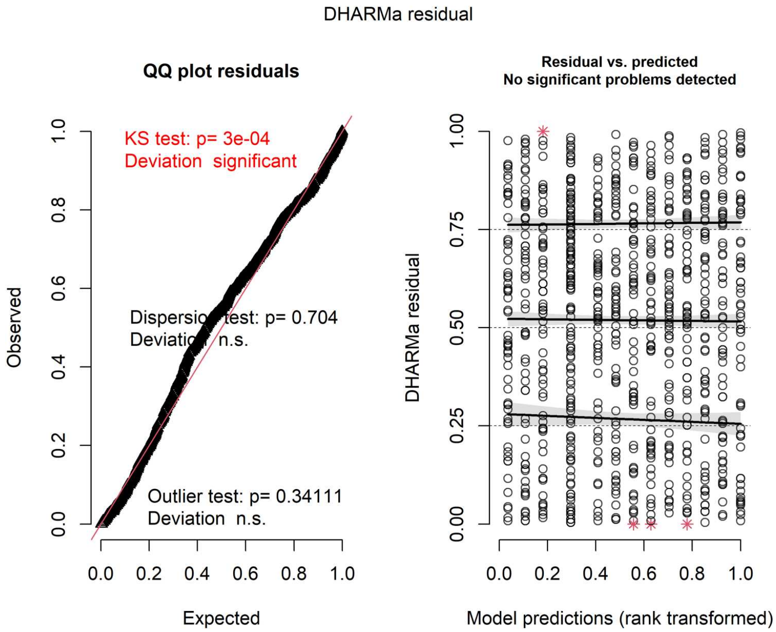
Models	Statistic	Intercept	treat EH1	treat EH2	treat MLS1	treat MLS2	treat LLS1	treat LLS2	treat SS1	treat SS2	treat TSSS1	treat TSSS2	treat TS1	treat TS2	height
Model for Mortality (Eq. 1)	Est.	3.3174	−0.7723	−0.5483	−0.3020	−0.3196	−0.5483	−0.7539	−0.9504	−0.5663	−0.3130	−0.0507	−0.9563	−0.8175	N/A
	Std.err.	0.4489	0.6074	0.6336	0.6717	0.6720	0.6336	0.6070	0.5878	0.6340	0.6720	0.7313	0.5880	0.6079	N/A
	z value	7.391	−1.272	−0.865	−0.450	−0.476	−0.865	−1.242	−1.617	−0.893	−0.466	−0.069	−1.626	−1.345	N/A
	p-value	1.46e-13	0.204	0.387	0.653	0.634	0.387	0.214	0.106	0.372	0.641	0.945	0.104	0.179	N/A
Model for GLD (Eq. 2)	Est.	35.0741	0.5398	−0.7456	−0.9111	−0.5823	−0.0925	0.6738	−1.5838	−0.6613	−0.6370	1.5444	1.4556	−0.0304	N/A
	Std.err.	1.2086	1.5858	1.5682	1.5601	1.5671	1.5683	1.5772	1.5958	1.5765	1.5682	1.5676	1.6055	1.5952	N/A
	z value	29.020	0.340	−0.475	−0.584	−0.372	−0.059	0.427	−0.992	−0.419	−0.406	0.985	0.907	−0.019	N/A
	p-value	2e-16	0.734	0.634	0.559	0.710	0.953	0.669	0.321	0.675	0.685	0.325	0.365	0.985	N/A
Model for height (Eq. 2)	Est.	243.92	8.3265	−4.5609	−2.3135	5.4670	7.4934	6.9160	−7.5345	10.738	4.0758	0.7595	2.8301	−12.721	N/A
	Std.err.	6.5710	8.0120	7.9228	7.8820	7.9171	7.9236	7.9685	8.0626	7.9650	7.9227	7.9202	8.1120	8.0597	N/A
	z value	37.12	1.04	−0.58	−0.29	0.69	0.95	0.87	−0.93	1.35	0.51	0.1	0.35	−1.58	N/A
	p-value	2e-16	0.299	0.565	0.769	0.490	0.344	0.385	0.350	0.178	0.607	0.924	0.727	0.114	N/A
Model for Quality: Occurrence of spike knots (Eq. 3)	Est.	−2.7074	0.5750	−0.1252	0.1986	−0.0462	−0.1782	−0.2872	−0.9729	0.1598	−0.7439	−0.0459	−0.1594	0.0958	0.4147
	Std.err.	0.4686	0.3775	0.4331	0.4008	0.4203	0.4333	0.4487	0.5711	0.4023	0.5259	0.4346	0.433	0.41	0.1554
	z value	−5.778	1.523	−0.289	0.496	−0.110	−0.411	−0.640	−1.704	0.397	−1.414	−0.106	−0.368	0.234	2.669
	p-value	7.58e-09	0.1277	0.7725	0.6202	0.9125	0.6809	0.5221	0.0884	0.6912	0.1572	0.9160	0.7128	0.8153	0.0076
Model for Quality: Occurrence of forks (Eq. 3)	Est.	−0.3998	−0.2231	0.4494	−0.2989	−0.1993	−0.5813	0.2938	−0.1340	−0.1729	−0.0321	0.2124	0.0048	0.4514	−0.0466
	Std.err.	0.3249	0.3264	0.3086	0.3239	0.3218	0.3406	0.3113	0.3246	0.3228	0.3231	0.3159	0.3151	0.3085	0.1094
	z value	−1.230	−0.684	1.456	−0.923	−0.619	−1.707	0.944	−0.413	−0.536	−0.099	0.672	0.015	1.463	−0.426
	p-value	0.2186	0.4942	0.1454	0.3561	0.5356	0.0878	0.3454	0.6799	0.5923	0.921	0.5014	0.9877	0.1435	0.6702
Model for Quality: Occurrence of bends (Eq. 3)	Est.	0.4221	1.18583	1.6203	0.0284	0.0883	0.5313	0.3701	−0.2002	0.4558	1.1146	1.8691	0.7155	1.9533	−0.2768
	Std.err.	0.3307	0.3321	0.3582	0.3068	0.3079	0.3089	0.3089	0.3175	0.3099	0.3336	0.3890	0.3122	0.3878	0.1134
	z value	1.276	3.571	4.524	0.093	0.287	1.720	1.2	−0.630	1.471	3.342	4.804	2.292	5.038	−2.440
	p-value	0.2018	0.0004	6.07e-06	0.9261	0.7744	0.0855	0.2302	0.5284	0.1414	0.0008	1.55e-06	0.0219	4.72e-07	0.014678

Notes: Eq. 1: Binomial GLMM; estimated value of $\sigma_{block} = 0.5755$. Eq. 2: LMM model. The estimated value of $\sigma_{block} = 1498$ and $\sigma_{block} = 44.13$ for H and GLD models respectively. The abbreviations appearing in the figure are TS (top shoot clipped), SS (side shoot clipped), TSSS (both clipped), MLS (moderate leaf stripping), LLS (low leaf stripping) and EH (an extra-heavy treatment combining MLS and TSSS). The numbers 1 and 2 indicate duration or number of years the treatments are applied.

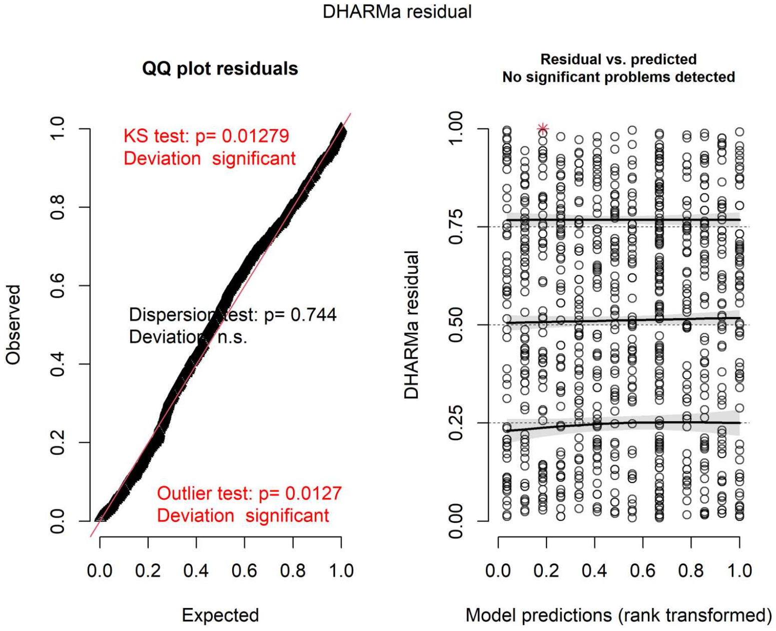
Appendix C. Residual plots generated by the DHARMa *package (*R Core Team *2024) for Eq. 1.*



*Appendix D. Residual plots generated by DHARMa package (*R Core Team *2024) for Eq. 2 (H).*



Appendix E. Residual plots generated by DHARMa package (R Core Team 2024) for Eq. 2 (GLD).



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Production of genetically improved silver birch plantations in southern and central Sweden

Liziniewicz M., Barbeito I., Zvirgzdins A., Stener L-G., Niemistö P., Fahlvik N., Johansson U., Karlsson B., Nilsson U. (2022). Production of genetically improved silver birch plantations in southern and central Sweden. Silva Fennica vol. 56 no. 1 article id 10512. 20 p. https://doi.org/10.14214/sf.10512

Highlights

- The basal area development of genetically improved birch in Sweden was modeled using a generalized algebraic difference approach.
- The best model fit, both graphically and statistically was delivered by the Korf base model.
- The analysis of realized gain trial showed a stability of relative differences in basal area between tested genotypes.

Abstract

Investing in planting genetically improved silver birch (*Betula pendula* Roth) in Swedish plantations requires understanding how birch stands will develop over their entire rotation. Previous studies have indicated relatively low production of birch compared to Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). This could result from using unrepresentative basic data, collected from unimproved, naturally-regenerated birch (*Betula* spp.) growing on inventory plots often located in coniferous stands. The objective of this study was to develop a basal area development function of improved silver birch and evaluate production over a full rotation period. We used data from 52 experiments including planted silver birch of different genetic breeding levels in southern and central Sweden. The experimental plots were established on fertile forest sites and on former agricultural lands, and were managed with different numbers of thinnings and basal area removal regimes. The model best describing total stand basal area development was a dynamic equation derived from the Korf base model. The analysis of the realized gain trial for birch showed a good stability of the early calculated relative differences in basal area between tested genotypes over time. Thus, the relative difference in basal area might be with cautious used as representation of the realized genetic gain. On average forest sites in southern Sweden, improved and planted silver birch could produce between 6–10.5 m^3 ha^{-1} $year^{-1}$, while on fertile agriculture land the average productivity might be higher, especially with material coming from the improvement program. The performed analysis provided a first step toward predicting the effects of genetic improvement on total volume production and profitability of silver birch. However, more experiments are needed to set up the relative differences between different improved material.

Keywords *Betula pendula*; generalized algebraic difference approach; genetic gain; planting; stand basal area starting function
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1 Introduction

Climate change is predicted to harm productivity of Norway spruce (*Picea abies* L. Karst) which has been the most commonly planted species in southern Scandinavia during the last century due to its economic potential (Kellomäki et al. 2008; Linnakoski et al. 2017). This potential is threatened by drought stress due to more frequent summer heat waves, which is likely to cause bark beetle outbreaks (Netherer et al. 2014). In addition, milder winters without frozen soil may increase the risk of windstorm damage and increase timber loss caused by root rot (*Heterobasidion* spp.). Consequently, broadleaved tree species, which may be more resistant to climate change, could be a valuable complement for the forest industry. Silver birch (*Betula pendula* Roth) is an obvious alternative to Norway spruce and Scots pine (*Pinus sylvestris* L.) since it is the third most abundant tree species in Swedish forests after these two conifers. Ecologically, silver birch has the broadest natural range of all European broadleaved species with extremely high phenotypic plasticity (Dubois et al. 2020). In addition, silver birch, like other deciduous tree species, whether in pure stands or mixed with other deciduous tree species, is less susceptible to wildfire damage than conifers (Pääkkönen et al. 1998; Ascoli and Bovio 2010; Terrier et al. 2013).

In the Nordic countries, birch (*Betula* spp.) is among the most productive of all commercially important native broadleaved species (Hynynen et al. 2010). The proportion of birch in the total standing volume of Swedish forests has continuously increased in recent decades due to the implementation of different environmental policies and certification schemes. Currently, birch makes up about 12.9% of the total volume in Sweden (Nilsson et al. 2021). Silver birch, the most abundant birch species in Sweden, often regenerates spontaneously and is retained in small proportions in forest stands dominated by Norway spruce or Scots pine. Naturally regenerated birch is of rather poor growth and quality as its management is often sub-optimal. For this reason, birch-wood is mainly used for pulp or fuel-wood in Sweden (Stener and Hedenberg 2003; Kilpeläinen et al. 2011), while only a very small proportion of birch wood is used as timber. Naturally regenerated birch is not usually managed for production of high-quality timber but to preserve the species throughout coniferous stands' rotation. Active management of birch could improve growth and timber quality, resulting in higher sawtimber production. This would economically offset its lower productivity compared to Norway spruce (Stener et al. 2017). The high-quality timber could also create a base for an industry for high-quality birch products as veneer industry in many countries of the Baltic Sea region, e.g. Finland (Viherä-Aarnio and Velling 2017), Latvia (Gailis et al. 2020) and Lithuania (Araminienė and Varnagirytė-Kabašinskienė 2014).

Using genetically improved birch is one way to increase growth and stem quality. Both traits have been significantly improved by the Swedish long-term breeding program (Stener and Jansson 2005) which started in the late 1980s (Rosvall 2011). The predicted genetic gain from the currently available seed-orchards is between 15% and 18% with significant improvement of the stem quality. However, interest in planting birch remains low. The annual production of birch seedlings in Sweden is marginal (ca. 1.3 million), compared to 400 million seedlings of Norway spruce and Scots pine combined (Skogsstyrelsen Statistical Database 2021). The low interest is mainly due to higher establishment costs and less production compared to Norway spruce. High establishment costs are mainly due to browsing pressure from large herbivores, especially moose (*Alces alces* L.) (Bergqvist et al. 2014). Studies using Swedish National Forest Inventory (NFI) data have shown that volume production capacity of naturally regenerated birch can be 40–60% lower compared to planted Norway spruce (Ekö et al. 2008). An estimation of productivity of planted birch stands have not been done in Sweden. The observation in the scattered birch experiments suggest that differences in relation to Norway spruce might be much lower than indicated by Ekö et al. (2008).

Better estimation of the productivity in the planted silver birch stands with improved material is essential for developing appropriate recommendation for the forest owners and for designing optimal management strategies (Bergquist et al. 2005). Better recognition of the production capacity might increase an interest in birch planting. The quantitative demonstration of the effect of breeding activities is also of great importance. Such quantification might be done by an implementation of the genetic gain from breeding programs into growth and yield models. The proposed alternatives that have been tested over the world are calculation of genetic gain multipliers, adjustment of site index (SI), and calibration of the model parameters (Weiskittel et al. 2011; Deng et al. 2020). These implementation efforts are strongly dependent on the availability of the proper experimental data that has been very rare in most of the breeding programs due to high costs of establishment, especially for species of low commercial interest such as birch (Sun et al 2004; Weiskittel et al. 2011). In addition, new generations of improved material are likely to be available before results from the experiments are available (Burkhart and Thome 2012; Egbäck et al. 2017; Deng et al. 2020). Consequently, by the time the tested genetic material reaches maturity, it might already be vanishing from commercial use (Haapanen et al. 2016).

However, other tools such as forest growth models can be used to show the effects of the breeding program, and to make long-term growth forecasts using a wide range of underlying experimental data. In this study, we analyzed the data from 52 available trials of silver birch in southern and central Sweden. The data set contained data from genetic trials from different phases of the breeding program as well as experiments established with a primary purpose of assessing growth and production with unknown genetic origin but with the high probability of being improved. The goal of the study was to develop a basal area development function for planted silver birch from this diverse material. The new function will be the first function for planted birch in Sweden. The currently available function has been fitted with data from the national forest inventory plots which often contain naturally regenerated and unmanaged birch and may underestimate volume production in the planted stands (Fahlvik et al. 2014; Elfving 2011). The secondary goal of the study was to present the stability of the genetic gain over time for silver birch. The hypothesis was that the gain calculated for volume and basal area later in rotation is at least of the same magnitude as early calculated gains in the selection age for height, diameter, basal area, and volume.

2 Material and methods

2.1 Data

The material for this study originated from 52 experiments with silver birch planted in southern and central Sweden between 1990 and 2010 on forest sites and former agricultural land (Table 1, Fig. 1). The average planting density was ca. 2500 trees ha^{-1}. The experiments were established using different statistical designs (single- and multi-tree plots), as they were established for different purposes, including studies of genetics, production and thinning. The calculations in this study were done on an experimental-plot level. The plot size ranged from 0.04 ha to 0.1 ha. Data from the plots established both on forest sites and former agricultural land was used as input for

Table 1. Mean, minimum (Min), maximum (Max) and standard deviation (SD) for variables describing the 52 thinned and unthinned periods from the silver birch experiments used in this study. Variables: BA is basal area; H_0 is the dominant height; SI is site index – the mean height of the 100 thickest trees per hectare at 50 years.

Variable	Unthinned (n = 301)				Thinned (n = 380)			
	Mean	Min	Max	S.D.	Mean	Min	Max	S.D.
t (years)	21	7	63	11	22	11	59	9
N (trees ha^{-1})	1506	302	2850	718	987	342	2160	387
BA (m^2 ha^{-1})	12.8	1.0	56.3	8.7	15.4	4.4	50.5	6.4
H_0 (m)	14.7	5.0	24.5	4.6	15.5	8.3	23.5	3.2
SI (m)	24.5	11.7	31.6	3.6	23.9	12.9	29.7	4.0

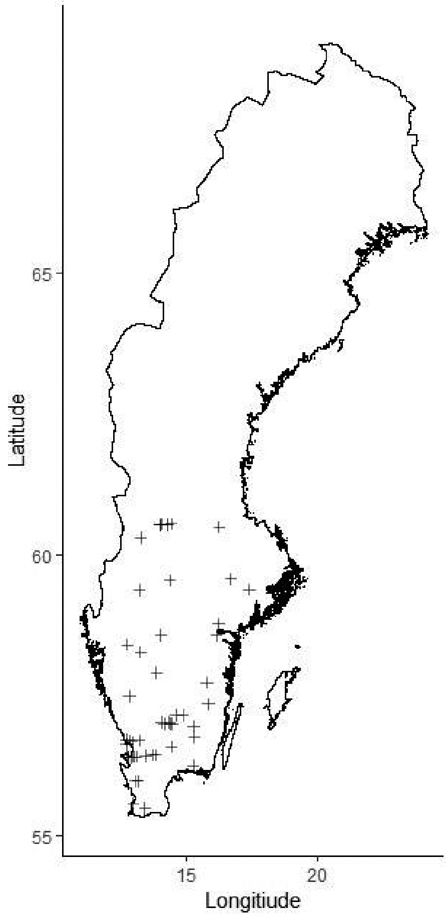

Fig. 1. Location of the silver birch study sites in Sweden.

construction of the models (Fig. 2). In total, there were 228 experimental plots. Each experiment was re-measured 2 to 7 times at 3–12 year intervals.

Stem diameter at breast height was registered for all trees at all measuring occasions. Height was recorded for the sample trees but not for all measurement occasions. Because of lack of data on heights, stand basal area was chosen as a dependent variable in the model as volume could not have been calculated for the intervals without height measurements.

The estimations of basal area and volume per hectare were based on the single tree measurements. A single tree height was estimated for the trees with measured diameter. The height estimation

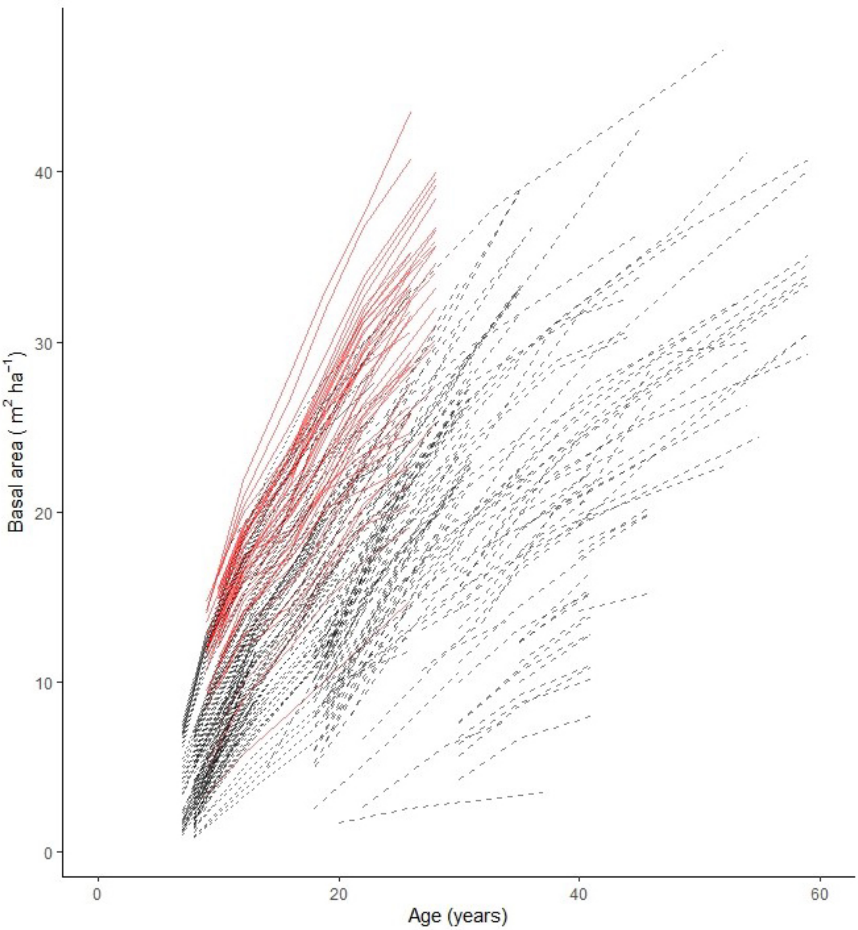

Fig. 2. Stand basal area growth data used for modelling basal area development of planted silver birch in Sweden. Experiments on former agriculture land are shown with solid (red) lines and on forest sites with dashed (black) lines.

was based on the height-diameter functions developed by Näslund (1936) with the power of three that resulted in the smallest residuals for the measured sample trees. The parameters of the Näslund (1936) function were calculated separately for plot or experiment depending on the number of sample trees available. The height of single tree with measured diameter have been consecutively estimated with the calculated parameters of the Näslund (1936) function. The volume of single tree was calculated with the functions developed by Brandel (1990).

Site index at the reference age of 50 years (Johansson et al. 2013) was calculated from age at breast height and top height (100 thickest trees ha^{-1}) for each experimental plot if heights of sample trees were measured. Top height was calculated out of the previously estimated heights. In general, the thinnings aimed to reduce the stem density by removing low-quality stems or competing trees but without a common pattern among the selected experiments. All the stands considered in this study have been thinned at least once as this is a common practice in birch plantation supporting the optimal stand growth. The thinning intensity ranged between 7% to 56% of basal area with the mean of 23%. Thinnings were done in the age between 11 to 26 years. The number of thinning were often three or less during the observation time, however, there was a variation both between experiments and between plots within experiments. Thus, it was assumed, that such thinnings resulted in negligible mortality. In addition, almost no mortality has been observed in the genetic field trials planted with an initial density of 2500 trees ha^{-1} at the time of diameter measurement between age of 7 and 12 years.

2.2 Overall approach

In this study we constructed a set of models to forecast the stand development of planted silver birch. We first developed a function to predict starting values (SV) of stand basal area in 7- to 12-year-old stands. This is the age when tree diameters are usually measured for the first time. Second, we developed a basal area development function using generalized algebraic difference approach (GADA). The best basal area development function was selected by statistically and graphically evaluating their goodness-of-fit. The starting values produced by the SV function were used to simulate basal area development over the full rotation with the selected basal area development function.

Lastly, we constructed a model to calculate stand form height (a ratio between total volume and basal area production) to estimate total volume production.

2.3 Stand basal area starting function (SV)

We developed a function to estimate the initial stand basal area at the starting age (between 7 and 12 years). At that age birch stands are usually well established and are approaching their first thinning. The linear model for prediction of initial basal area included independent variables of age (years), stand density (square root-transformed number of trees ha^{-1}) and site index in meters at the reference age of 50 years (Johansson et al. 2013). The dependent variable was logarithmically transformed such that the model error terms were normally distributed and to reduce heteroscedasticity of the error variance. The starting values of the estimated basal area were then used as input for further basal area development.

2.4 Basal area projection function (BAP)

Three different well known growth functions were tested and selected for evaluation during the process of stand basal area function development. Among the candidate functions were: Korf

(BA1 and BA2) (Korf 1939), Hossfeld (BA3 and BA4) (Cieszewski and Zasada 2002 as cited in Cieszewski et al. 2007 and McDill and Amateis 1992 as cited in Anta et al. 2006), and Bertalanffy-Richards (BA5 and BA6) (von Bertalanffy 1949 as cited in Liziniewicz et al. 2016) (Table 2). The tested functions included recently developed dynamic equations with two site-specific parameters and frequently used dynamic equations with only one site-specific parameter (Castedo-Dorado et al. 2007). As all the plots were thinned at least once, the functions were fitted to all the growth intervals.

The fitting procedure followed the dummy variable method proposed by Cieszewski and Bailey (2000) which models site index and stand development with the algebraic difference approach (ADA) and generalized algebraic difference approach (GADA). The fitting procedure was programmed in R version 3.6.1 using the *nls* procedure (R core Team 2019).

2.5 Volume function (VF)

A function incorporating stand height was developed to estimate volume (m^3 ha^{-1}) from basal area (m^2 ha^{-1}) values (Eq. 1). This allowed making the basal area development model more useful, as volume is the fundamental unit used in forestry practice. To develop this function, we used data from experimental plots, where total volume production per hectare was estimated. The ratio between total volume production per hectare and total basal area production per hectare (response variables) was modelled as a linear function against top height (average height of 100 thickest trees per ha^{-1}) and age (explanatory variables X_1 and X_2):

$$\frac{Vol}{BA} = a_1 X_1 + a_2 X_2 + \varepsilon, \tag{1}$$

where *Vol* is volume per hectare (m^3 ha^{-1}); *BA* is basal area per hectare (m^2 ha^{-1}), a_1 is the intercept, a_1 is the coefficient for independent variable X_1, a_2 is the coefficient for independent variable X_2, and ε is a random error term $N(0, \sigma^2)$. In the simulation, we transformed basal area into volume by multiplying the right side of the equation by basal area.

2.6 Model fitting and model evaluation

The quality of the fitted BAP, SV and VF functions was evaluated both graphically and numerically. For the models, standardized residuals were visually assessed to detect any remaining pattern with respect to the explanatory variables. The numerical analysis consisted of calculation of goodness-of-fit statistics: the root mean squared error (RMSE), which gives the accuracy of the estimates in the same units as the dependent variable, and the coefficient of determination (e.g. pseudo-R^2 when applied in non-linear regression), which is the proportion of the total variance of the dependent variable explained by the model.

Validation of the models was carried out using an independent dataset from experiments in Finland. The dataset originated from thinning experiments established on twelve different experimental sites in southern and central Finland with observation periods of 16–48 years. Different thinning practices were applied to plots within the experiments. Measurements of the thinning experiments were similar to the Swedish data used for the construction of the models. Stem diameter was measured at breast height for all trees within the experimental plots. Total basal area production per hectare including harvested trees and mortality was calculated for individual plots. Models were validated by both statistical and graphical inspection of basal area development in the thinning experiments compared to the projected basal area development from the best BA development function. The following numerical statistics were calculated:

Table 2. Base models and Generalized Algebraic Difference Approach (GADA) forumulations selected for basal area development of silver birch.

Base model	Parameter related to site	Solution for x with initial values (t0, Y0)	Dynamic equation	Model name
Korf	$a_2 = X$	$X_0 = -\ln\left(\frac{Y_0}{a_1}\right)t_0^{a_3}$	$Y = b_1\left(\frac{Y_0}{b_1}\right)^{\left(\frac{t_0}{t_1}\right)^{b_3}}$	BA1
$Y = a_1 \exp\left(-a_2 t^{-a_3}\right)$	$a_1 = \exp(X)$ $a_2 = b_1 + b_2 / X$	$X_0 = \frac{1}{2}t_0^{-b_3}\left(b_1 + t_0^{b_3}\ln(Y_0) + \sqrt{4b_2 t_0^{b_3} + \left(-b_1 - t_0^{b_3}\ln(Y_0)\right)^2}\right)$	$Y = \exp(X_0)\exp\left(-(b_1 + b_2 / X_0)t^{-b_3}\right)$	BA2
Hossfeld	$a_2 = X$	$X_0 = t_0^{-a_3}\left(\frac{a_1}{Y_0} - 1\right)$	$Y = b_1 / \left(1 - (1 - b_1 / Y_0)(t_0 / t)^{b_3}\right)$	BA3
$Y = \frac{a_1}{1 + a_2 t^{-a_3}}$	$a_1 = b_1 + X$ $a_2 = b_2 / X$	$X_0 = \frac{1}{2}\left(Y_0 - b_1 + \sqrt{(Y_0 - b_1)^2 + 4b_2 Y_0 t_0^{-b3}}\right)$	$Y = \frac{b_1 + X_0}{1 + b_2 / X_0 t^{-b_3}}$	BA4
Bertalanffy-Richards	$a_2 = X$	$X_0 = -\ln\left(1 - \left(\frac{Y_0}{b_1}\right)^{\frac{1}{b_3}}\right) / t_0$	$Y = b_1\left(1 - \left(1 - \left(\frac{Y_0}{b_1}\right)^{\frac{1}{b_3}}\right)^{\frac{t}{t_0}}\right)^{b_3}$	BA5
$Y = a_1$	$a_1 = \exp(b\|1)$ $a_2 = b_2 + b_3 / X$	$X_0 = -\ln\left(1 - \left(\frac{Y_0}{b_1}\right)^{\frac{1}{b_3}}\right) / t_0 X_0 = \frac{1}{2}\left(\ln Y_0 - b_2 L_0 + \sqrt{(\ln Y_0 - b_2 L_0)^2 - 4b_3 L_0}\right)$ with $L_0 = \ln\left(1 - \exp(-b_1 t_0)\right)$	$Y = Y_0\left(\frac{1 - \exp(-b_1 t)}{1 - \exp(-b_1 t_0)}\right)^{(b_2 + b_3 / X_0)}$	BA6

Root mean square (RMSE):

$$RMSE = \sqrt{\sum_{i=1}^{n} \frac{\left(\widehat{Y}_i - Y_i\right)^2}{n}}$$

Mean absolute error (MAE):

$$MAE = \frac{1}{n} \sum_{i=1}^{n} \left| Y_i - \hat{Y}_i \right|$$

Modelling efficiency coefficient:

$$ME = 100 \times \left(1 - \frac{\sum_{i=1}^{n} \left(Y_i - \hat{Y}_i \right)^2}{\sum_{i=1}^{n} \left(Y_i - \overline{Y}_i \right)^2} \right)$$

where Y_i is a trait value, $\overline{Y}_i$ is a mean value of the trait, $\hat{Y}_i$ is an estimate of the trait and i is an indication of the measurement.

With the developed functions a simulation of the results for four sites at site indices B22, B25, B28 and B32 defined as a top height in meters in the age of 50 years were done. The stocking of the simulated stands were 2200 stems per hectare in the initial age of 10 years. The initial basal area was calculated using the SV model. Subsequently, the BAP function was used to project stand development followed by a transformation of basal area into volume using VF function. Three thinnings were applied to each stand and thinning time differed depending on SI and were applied earlier for higher site index. In each thinning 30% of basal area was removed. The basal area predictions were done until the Land Expectation Value (LEV) reached the maximum:

$$LEV = NPV \times \frac{(1+\iota)^u}{(1+\iota)^u - 1}; \qquad NPV = \sum_{t=0}^{n} \left(\frac{R_t}{(1+i)^t} \right) \tag{2}$$

where NPV is net present value (Eq. 2), R_t is net cash inflow-outflow during a single period t, n is the number of time periods, i is the discount rate and u is rotation age. The LEV as well as other monetary values were first calculated in SEK, and converted to EUR by using an exchange rate 0.096 (European Central Bank 2020).

The cost of establishment was set to 1440 EUR ha^{-1}. All volume produced was treated as pulpwood with a price of 33.6 EUR m^{-3}. Harvesting costs (in EUR m^{-3}) of thinning operations and final felling were estimated based on average costs of these activities in southern Sweden between 2005–2015 (Nilsson et al. 2016).

2.7 Realized gain

The experiment S21S9331222 in Jordkull in southern Sweden (59°34´N, 14°15´E) is the only one Swedish birch experiment where clones of 10 genotypes were planted plot wise i.e. a single plot contains just one genotype. The experiment might be considered as a realized gain trial. Such type of trials is also rare for other tree species. It was planted in 1993 with cloned plants with known genetic background. However, planted genotypes in the trial have not been intended for a deployment to the operational forestry.

In this study, the experiment was used to investigate if between genotype variation in different stand properties is stable over time. The relative differences between genotypes were calculated for height, diameter and stand basal area at the age of 9 years and were presented in relation to the relative differences in total basal area production, total volume production and site index in the last measurement occasion i.e., 26 years. The worst performing genotype has been used as a reference for testing the realized gain of the other genotypes, resulting in an approach of the gain over unimproved material.

3 Results

3.1 Basal area starting function and the volume function

The initialization function consisting of age (years), stand density (square root-transformed number of trees ha^{-1}) and site index as independent variables explained 64% of the total variance of basal area with an RMSE of 0.38 m^2 ha^{-1} (Table 3). Model residuals were normally distributed with some detectable trends especially for for the lower predicted values of basal area and site index (Supplementary file S1, available at https://doi.org/10.14214/sf.10512). Despite of a range of applied transformation, the heteroscedasticity could not be removed.

The linear model predicting stand form height i.e., ratio between total volume and basal area production, explained 94% of the total variance with an RMSE of 0.49 m (Table 4). Residual analysis revealed no trends over the dependent or independent variables (top height and age) (Suppl. file S2).

Table 3. Parameter estimates of initial conditions in the stand values of silver birch. SE is standard error, t-values and p-values demonstrate the statistical performance of the parameters. The model is based on a dependent variable of logarithmically transformed basal area for stands between 7 and 12 years old and several independent variables: age (years), quadratic square root-transformed number of trees (N ha^{-1}) and site index (SI) at 50 years (Johansson et al. 2013).

	Estimate	SE	t-value	p-value
Intercept	–7.3193	0.8710	–8.40	3.19e^{-14}
Age (years)	0.2138	0.0151	14.11	2e^{-16}
(N ha^{-1})	0.0643	0.0188	3.42	0.000814
Site index (m)	0.1555	0.0152	10.23	< 2e^{-16}

3.2 Basal area development function

The two- and three-parameter models derived from the Korf´s base function performed similarly between 0 and 40 years (Fig. 3). These functions also explained the greatest share of the total variation (>97%) and resulted in the lowest root mean square error (RMSE, Table 4). The function with three parameters derived from the Bertalanffy-Richards base model was similar in terms of quality of fit (Table 5). However, this model explained a slightly lower share of variation and had a greater RMSE, whereas the two-parameter function derived from the same base model function performed similarly to the three-parameter function up to a basal area of 40 m^2 ha^{-1}. The three-parameter function derived from Hossfeld´s base model performed poorly when the basal area exceeded 30 m^2 ha^{-1}. The Korf function performed the best both statistically and visually, so it was selected for further analysis. The trajectory of the modeled curves of the Korf models encompassed the actual growth pattern of the observed values (Fig. 3). Out of the two final functions (BA1 and

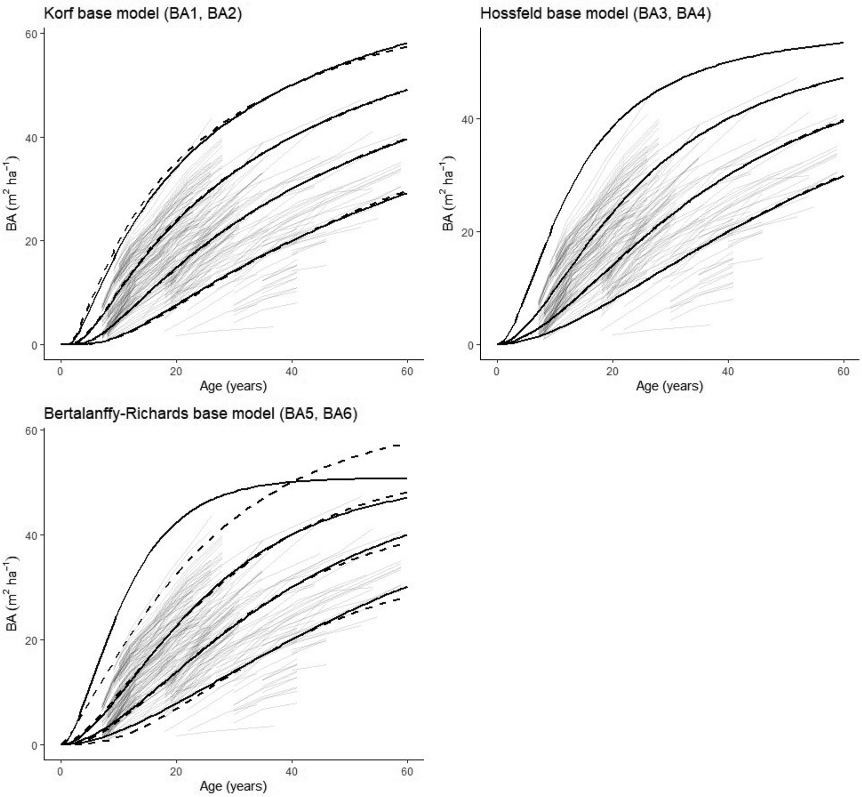

Fig. 3. Basal area development curves of silver birch reaching basal areas of 15, 25, 35 and 45 m^2 ha^{-1} at 40 years for the two-parameter models (BA1, BA3, BA5 – solid lines) and the three parameter models (BA2, BA4, BA6 – dashed lines).

Table 4. Parameter estimates for the model converting basal area into volume for silver birch. The dependent variable is a ratio between total volume production and total basal area production. Independent variables are top height (m) and age (years). SE is standard error, t-values and p-values demonstrate the statistical performance of the parameters.

	Estimate	SE	t-value	p-value
Intercept	–0.4044	0.063	–6.45	<0.05
Top height (m)	0.4286	0.006	75.2	<0.05
Age (years)	0.0085	0.002	3.65	<0.05

BA2), the two-parameter function with one site-specific parameter (BA1) was selected because of its more parsimonious nature compared to BA2 and slightly better goodness-of-fit statistics (Table 5). Furthermore, residual analysis showed the residuals were evenly distributed around zero, with homogeneous variance and no detectable trends.

3.3 Model validation

The BA1 function was validated against data from thinning experiments in Finland. The root mean squared error was 1.42 $m^2 ha^{-1}$ while mean absolute error was 0.22 $m^2 ha^{-1}$. The modelling efficiency was ca 93%. A visual inspection showed good visual conformity between the model and Finnish thinning experiments. The modeled curves were well matched to the measured pattern of basal area development (Fig. 4). However, even though the model showed good performance visually and in terms of fit statistics, residual analysis revealed that there was slight tendency for a bias (Suppl. file S3). The t-test comparing observed and predicted basal area values did not reveal a significant bias ($p=0.3645$). Even though the majority (75%) of residuals fell within ±2 $m^2 ha^{-1}$ of the measured basal area, the residual values appeared to increase with the predicted total basal area, indicating increasing over-prediction of basal area over longer timescales.

Table 5. Parameter estimates, standard errors (SE), and goodness-of-fit measurements (P = level of statistical significance, RMSE = root mean square error, R^2 = coefficient of determination) for the dynamic equations for basal area development of silver birch considered in this study.

Base model	Parameter	Estimate	SE	P	RMSE	R^2
Korf (BA1)	$b_1 b_2$	91.3397 0.7054	6.2864 0.0296	<0.0001 <0.0001	1.569	0.9724
Korf (BA2)	$b_1 b_2 b_3$	506.8 –1900 0.5985	325.0 1472 0.302	0.119 0.127 <0.0001	1.568	0.9726
Hossfeld (BA3)	$b_1 b_2$	57.1328 1.7511	2.1663 0.04	<0.0001 <0.0001	1.754	0.9656
Hossfeld (BA4)	$b_1 b_2 b_3$	59.1606 –552.77 –1.7460	3.4204 851.43 0.03987	<0.0001 0.516 <0.0001	1.755	0.9656
Bertalanffy-Richards (BA5)	$b_1 b_2$	50.7827 1.9404	1.5410 0.0615	<0.0001 <0.0001	1.7522	0.9351
Bertalanffy-Richards (BA6)	$b_1 b_2 b_3$	0.0458 –10.2369 47.6122	0.0022 2.1422 8.2858	<0.0001 <0.0001 <0.0001	1.663	0.9691

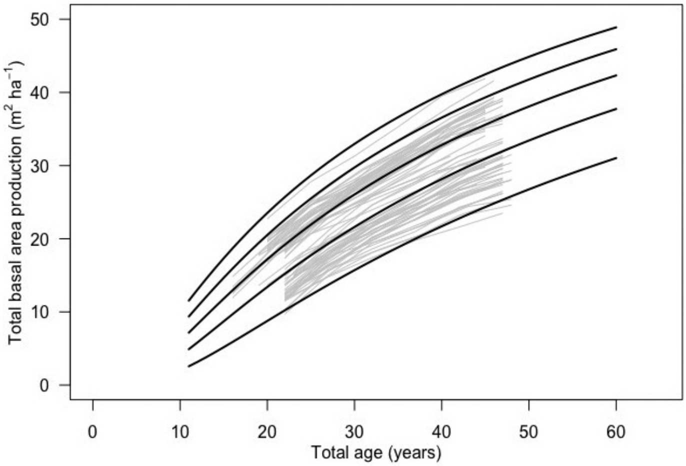

Fig. 4. Basal area development of silver birch in 12 thinning experiments in Finland (gray lines) and basal area development according to the Korf function (BA1; black lines).

3.4 Models' application

The application of the models into four stands with different site indices (SI) with stocking of 2200 trees ha^{-1} in 10 years showed an increase of mean annual increment (MAI) and a decrease of the optimal rotation age with increasing SI (Table 6). The rotation age at the best site was 31 years with the MAI of 12.8 m^3 ha^{-1} year^{-1}.

Table 6. Results of the simulation for silver birch stands established with planting material with site indices of 22 m, 25 m and 28 m at 50 years. Initial stand density is 2200 trees ha^{-1} at 10 years. Three thinnings (including one non-commercial cleaning and two commercial thinnings) with removal of 30% of basal area were applied in each stand. Land expectation value (LEV) based on a 2.5% discount rate was applied.

Site index	Mean annual increment	Land expectation value	Rotation length	Harvested volume Thinning	Harvested volume Final felling
(m)	(m^3 ha^{-1} year)	(EUR ha^{-1})	(years)	(m^3 ha^{-1})	(m^3 ha^{-1})
22	6.0	479.6	60	93	269
25	7.9	1511.7	51	66	337
28	10.5	3103.2	45	80	394
32	12.8	5500.8	31	108	287

Table 7. Relative differences between silver birch genotype German 2 and other silver birch genotypes for height (H), diameter (D), top height (TH), site index (SI), basal area (G) and volume (V). The number indicate an age when the trait was measured.

Origin	H_9	D_9	G_9	V_9	TH_9	SI_26	G26	V_26
E-län (Sweden)	120%	108%	124%	140%	117%	107%	113%	132%
Ekebo 1 (Sweden)	125%	118%	153%	180%	126%	110%	155%	183%
Finland 1	115%	110%	128%	140%	112%	105%	125%	137%
Finland 2	133%	115%	144%	179%	127%	111%	136%	162%
Holland	130%	117%	148%	179%	118%	108%	103%	110%
Latvia	127%	121%	157%	186%	128%	112%	146%	175%
Mixed	108%	107%	89%	95%	115%	107%	100%	117%
T-län	131%	125%	170%	206%	136%	115%	188%	252%
German 1	111%	121%	132%	137%	113%	106%	123%	136%
German 2	100%	100%	100%	100%	100%	100%	100%	100%
Average (1:9)	122%	116%	138%	160%	121%	109%	132%	156%

3.5 Quantification of relative differences in genotypes performance

The Genotype indicated as the German2 was the worst performing and it has been used as a reference. The relative differences in the age of 9-years-old between the worst genotype and average were 22 % and 16% for height and diameter, respectively. The relative basal area differences decreased slightly from age of 9 years to the age of 26 years (Table 7, Fig. 5). The difference between basal area for both ages was in a range of 20% and the difference was increasing with an increase of an initial gain at age of 9 years. One exception was the genotype from Holland which with age lost all the gain in basal area it has at the age of 9 years i.e. 45%. The simple correlation between age 9 years and age 26 years for differences in basal area was 0.77 and for basal area at age 9 years and volume at age 26 years the correlation coefficient was 0.72.

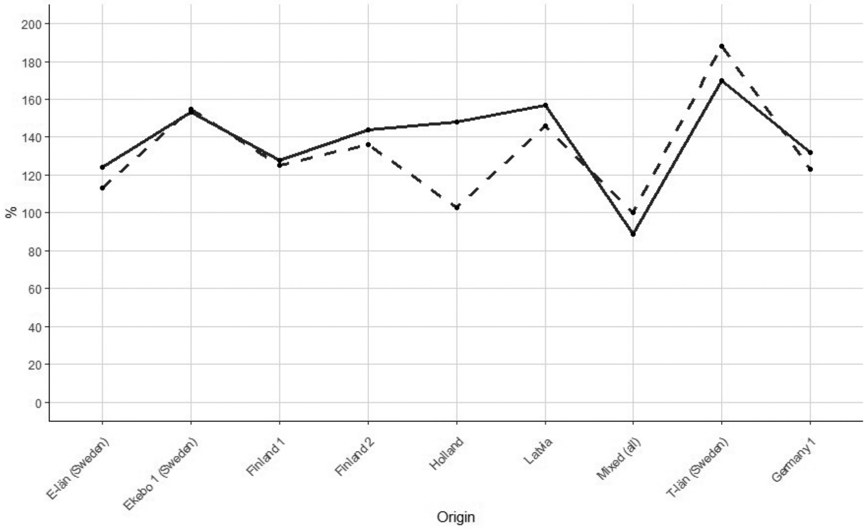

Fig. 5. Relationship between relative difference in basal area of silver birch between genotype German 2 and other genotypes in the age of 9 years (solid line) and 26 years (dashed line). Correlation between relative difference in age 9 years and 27 years was 0.77 (German 2 was excluded).

4 Discussion

4.1 Model fit and validation

In this study, the two-parameter Korf function with one site-specific parameter was selected for modelling silver birch basal area development. The function includes age, stocking level and SI, and was selected for its parsimony and good performance over the observed growth trajectories obtained from 52 field trials. SI in the SV model was used to account for the genetic gain. The selected function showed good predictive ability and represented the experimental data accurately over the potential 40 year rotation age for planted silver birch in southern Sweden. In addition, the function provided reliable estimates even beyond the presented time span, up to 60 years.

Validation of the selected model using an independent dataset from Finnish thinning experiments showed that the model accurately forecasts the observed growth in basal area. However, certain shortcomings were observed, particularly an increasing over-prediction of the basal area over longer timescales, which indicates that the model needs to be used with caution when applied for longer periods. Moreover, our model provides useful estimates of total stand basal area development. However, forecasting tree mortality is impractible as the mortality function was not included in the models constructed in this study.

4.2 Planted stand productivity

The production of planted silver birch stands is clearly higher than values previously calculated using data from NFI plots (Ekö et al. 2008). The estimates of this study show that the stands planted with the available silver birch planting material (at the time of planting) on average-fertility forest sites in southern Sweden resulted in MAI's of 6–12.8 m^3 ha^{-1} $year^{-1}$. With a new improved material, there is a potential for further increases stand productivity in the future as the most improved material that is currently available has not been used for establishment of the analyzed plots. According to Dahlberg et al. (2006), the MAI of silver birch on fertile sites in Sweden is ca. 10 m^3 ha^{-1} $year^{-1}$ for rotations between 30 and 60 years. Similar productivity was suggested based on current annual increment (CAI) observation for stands on agriculture land in southern Sweden where CAI was estimated in temporary sample plots (Sonesson et al 1994). Our analysis of the realized gain trial planted on fertile site with improved genetic material showed that production can reach up to 14 m^3 ha^{-1} $year^{-1}$. The productivity predicted by the basal area development model for fertile site of SI 32 meters in 31 years were 12.8 m^3 ha^{-1} $year^{-1}$. This indicates that silver birch production can approach levels achieved with planted Norway spruce if genetically improved birch is planted. However, since there is also an ongoing breeding program for Norway spruce with similar objectives, it is unlikely that the difference in production between the two tree species will be fully eliminated in the near future (Egbäck et al. 2017). In order to compare Norway spruce, silver birch and other species, there is a need for more controlled experiments testing genetically superior material of different species.

4.3 Current genetic gains and a future of silver birch breeding in Sweden

The current genetic gains for a specific deployment material of silver birch are estimated based on the parameters calculated for other tree species i.e., age to age correlations between selection e.g., diameter and height and objective traits e.g., volume production over rotation. This is done due to the lack of experiments for Silver birch, while there are many existing experiments for Norway spruce and Scots pine. Hence, the realized genetic gain might be larger than predicted.

For instance, the Finnish silver birch breeding program showed a genetic volume gain of up to 30% over the full rotation period for the same type of tested plus trees (Hagquist and Hahl 1998; Pöykko 2018). The analysis in this study done in the single realized gain trial showed the differences in basal area production in 26 years between worst and average among randomly selected and propagated clones reached 32% and was stable over time except a genotype from Holland. In this case, the difference is most likely related to a long north-transfer distance of this material.

The calculated difference cannot directly be perceived as a genetic gain in relation to unimproved material but gives a good indication that early measured differences between genotypes might be a reliable estimation of genetic superiority. The stability of the differences over time are in line with the studies for Norway spruce in Sweden where early measured differences between unimproved and improved seed lots persisted up to first thinning (Liziniewicz et al. 2018). The greater relative differences in volume per hectare productivity also indicate that selection of certain genetic material affect height development. Thus, adjustment of both basal area and height is needed to incorporate appropriately genetic gain to growth and yield models.

4.4 Limitations of this study

The design behind available experimental data is the main limitation of this study. The genetic experiments mainly used a single-tree plot design, where a mixture of genotypes from several families are randomly planted over the experimental area. Plots containing just one deployment material would be preferrable but were not available.

Moreover, experiments had different levels of genetic improvement, including 1) older thinning experiments established in stands of unknown genetic background, 2) stands planted for production studies using material of different provenances, 3) genetic trials of the basic selection of plus trees, 4) genetic trials with well performing selected material, and 5) provenance trials and production trials using deployment material (i.e., plants originating from available seed orchards). Thus, the genetic variation was substantial and not controlled in this study as the approach assumed that the newly developed curves will represent a mean of all birch stands established with improved material.

Another limitation of the constructed model is that the starting values are affected by initial stand density and this has little to do with fertility or tree performance. Therefore, the models are only valid within the relatively limited range of initial stocking represented in our data (1800–2200 trees ha^{-1}).

5 Conclusions

The main objective of this study was to construct a stand basal area development model for planted silver birch in southern and central Sweden based on available data. These development functions have proven reliable, with an ability to accurately predict basal area development of silver birch stands over a range of site fertilities in southern and central Sweden. Validation of the basal area development functions using an independent dataset from thinning experiments in Finland showed good fit; however, it must be noted that when applied outside of its geographical scope, the model should be used with caution. The analysis of realized gain trial showed that planting improved silver birch material will increase stand productivity, and consequently shorten stand rotations and improve stand profitability considerably, particularly on fertile sites. Further studies including wood quality traits and financial analyses would be required to demonstrate how genetically improved birch can become a viable complement to Norway spruce and Scots pine in Sweden. A series of realized gain trials to confirm genetic gain of the deployment material and calibration of the models would be valuable for future analysis of production and economy in planted birch.

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Availability of research materials and data

The research materials and data used in this study are available upon reasonable request.

Supplementary files

S1.pdf; Residuals of the basal area starting function vs. independent variables,
S2.pdf; Residuals of the volume model vs. observed independent variables,
S3.pdf; Residuals of the BA1 model vs. predicted values using an independent dataset,
available at https://doi.org/10.14214/sf.10512.

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This thesis investigated how spacing, browsing, thinning, and genetic improvement influence the establishment and growth of planted silver birch. The results showed that the use of genetically improved planting material substantially enhanced stand productivity, but establishment and management choices proved crucial. Browsing had little effect on survival or height of silver birch, but tree quality was reduced, warranting protection where risk is high. Thinning promoted diameter growth, with heavier thinning favouring large trees at the expense of overall volume production.

Andis Zvirgzdins received his PhD education at the Southern Swedish Forest Research Centre, Swedish University of Agricultural Science (SLU), Alnarp. He obtained his MSc degree in Forest Science through the Euroforester Master's programme at SLU, Alnarp, and his BSc in Forest Engineering from the Latvia University of Agriculture (LUA).

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