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Cover: The multifaceted approach to establishing poplar in acidic soils in Sweden (photos by Luca Muraro)

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Fast-growing broadleaved alternatives for Swedish forestry - Overcoming challenges on the establishment of *Populus* species

Abstract

Swedish forestry is undergoing a transition towards more diverse and climate-resilient production systems. Fast-growing broadleaved species, particularly hybrid poplars, offer high productivity and short rotations, but their establishment on acidic forest soils remains a major constraint. This thesis investigates strategies to overcome these barriers by combining species-site matching, genetic screening for aluminium (Al) tolerance, and soil amendment trials, supported by a systematic literature review. Four complementary approaches were applied. First, a multi-species field comparison across forest and forested arable land revealed strong site-dependent establishment patterns. Hybrid aspen and silver birch performed best on forest soils, whereas poplars required ash treatment to succeed on forested arable land. Second, a screening of 70 poplar clones demonstrated substantial genotypic variation in Al tolerance, with height showing moderate heritability ($H^2 \approx 0.45$). A Composite Tolerance Index (CTI) integrating clonal growth responses and genetic merit identified tolerant clones capable of maintaining performance in acidic soils. Third, multi-site field trials tested wood ash, lime, and biochar amendments, showing that ash improved survival and growth most consistently, although effects varied with site type and application method. Finally, a systematic review of 41 studies confirmed that wood ash generally enhances growth of broadleaved species on acidic or nutrient-poor soils, but responses are context-dependent and often moderated by dose and soil type. Together, these findings highlight a dual-track strategy for deploying poplars in Swedish forestry: (i) the selection and breeding of Al-tolerant clones, and (ii) the targeted use of soil amendments, particularly wood ash, where genetic tolerance alone is insufficient. This integrated approach can expand the cultivation of fast-growing broadleaves beyond fertile farmland into underutilized forest soils, contributing to diversification, climate adaptation, and sustainable wood supply.

Keywords: *Populus*, poplar, hybrid aspen, aspen, aluminium tolerance, soil amendments, wood ash, forest diversification, establishment, fast-growing broadleaves

Snabbväxande lövträdsalternativ för svenskt skogsbruk - att övervinna etableringsutmaningar för Populus-arter

Abstract

Det svenska skogsbruket genomgår en omställning mot mer diversifierade och klimatresilienta produktionssystem. Snabbväxande lövträd, särskilt poppelhybrider, erbjuder hög produktivitet och korta omloppstider, men deras etablering på sura skogsjordar utgör en stor begränsning. Denna avhandling undersöker strategier för att övervinna dessa hinder genom att kombinera arts- och markanpassning, genetisk screening för aluminiumtolerans samt fältförsök med markförbättringar, kompletterat med en systematisk litteraturöversikt. Fyra kompletterande angreppssätt tillämpades. För det första visade en fältjämförelse mellan flera trädslag på skogs- respektive åkermarker tydliga markberoende etableringsmönster. Hybridasp och vårtbjörk presterade bäst på skogsmark, medan poppelkrävde askbehandling för att lyckas på åkermark. För det andra visade en screening av 70 poppelkloner stor genetisk variation i tolerans mot aluminium, där höjd uppvisade måttlig heritabilitet ($H^2 \approx 0,45$). Ett sammansatt toleransindex (CTI), som integrerade klonernas tillväxtrespons och genetiska värde, identifierade toleranta kloner som kunde bibehålla sin tillväxt på sura jordar. För det tredje testades vedaska, kalk och biokol i flerplatsförsök, där vedaska gav de mest konsekventa förbättringarna i överlevnad och tillväxt, även om effekten varierade med marktyp och spridningsmetod. Slutligen visade en systematisk översikt av 41 studier att vedaska i regel förbättrar tillväxten hos lövträd på sura eller näringsfattiga marker, men att responsen är kontextberoende och ofta påverkas av dosering och marktyp. Sammantaget pekar resultaten på en dubbel strategi för etablering av poppel i svenskt skogsbruk: (i) selektion och förädling av aluminiumtoleranta kloner, och (ii) riktad användning av markförbättringar, särskilt vedaska, där genetisk tolerans ensam inte är tillräcklig. Denna integrerade metod kan möjliggöra odling av snabbväxande lövträd utanför bördiga åkermarker och därigenom bidra till ökad diversifiering, klimatanpassning och en hållbar virkesförsörjning.

Keywords: *Populus*, poppel, hybridasp, asp, aluminiumtolerans, markförbättringar, vedaska, skogsdiversifiering, etablering, snabbväxande lövträd

Dedication

To coffee, sarcasm, and Nora. Two kept me awake, one kept me going

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. **Muraro, L*.**, Robinson, K. Liziniewicz, M., Böhlenius, H. (2025). Establishment of fast-growing tree species on forest and former agricultural land in Northern Europe – implication for forest diversification. (submitted)

II. **Muraro, L*.**, Liziniewicz, M., Robinson, K., Pohl, N., Adler, A., Böhlenius, H. Screening and selection of aluminium-tolerant *Populus* genotypes for acidic soil conditions. (manuscript)

III. **Muraro, L.**, Adler, A., Böhlenius, H.* (2025). Effect of Wood Ash, Lime, and Biochar on the Establishment and Early Growth of Poplars on Acidic Soil Conditions. BioEnergy Research, Volume 18, (29), https://doi.org/10.1007/s12155-025-10831-1

IV. Puurula, I., González Orenga, S, Svystun, T, **Muraro, L**., A. Felton, M. Ohman, Böhlenius, H.*, Does ash increase the growth of boreal and temperate broadleaved tree species? – a systematic review. (manuscript)

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The contribution of Luca Muraro to the papers included in this thesis was as follows:

I. **LM** developed the research idea together with HB. **LM** participated in planning, establishment of experimental sites, conducting fieldwork for data collection. **LM** conducted the statistical analyses together with KR and took the main responsibility in developing the figures and interpretation of the results. **LM** wrote the first draft manuscript and developed it further collaboration with all other co-authors.

II. **LM** developed the research idea together with HB. **LM** planned the experiment together with HB and conducted fieldwork together with NP. **LM** conducted the statistical analyses together with NP and took the main responsibility in data analysis and display of the results. **LM** interpreted the results and wrote the first draft of developed it further collaboration with all other co-authors.

III. **LM** developed the research idea together with HB. **LM** took part in establishment of experimental sites and conducting fieldwork for data collection. **LM** conducted the statistical analyses, outline of the figures and wrote the draft of the manuscript and developed it further in collaboration with all other co-authors.

IV. IP developed the research idea together with **LM**, TS, SGO, AF and HB. IP conducted the literature searches. IP, **LM**, TS and HB performed the initial paper screening. Final paper reading and data collection were performed by IP. IP, TS, **LM**, SGO, AF and HB developed the first draft of the manuscript. All authors contributed to the final version of this manuscript.

List of figures

Abbreviations

AL	Ammonium Lactate (soil extraction method)
Al^{3+}	trivalent Aluminium
ArFor	Forested arable land (former agricultural land)
AT	Ash-treated (Poplar seedlings treated with wood ash)
AUC	Area Under the Curve
BLUP	Best Linear Unbiased Prediction
BS	Base Saturation
CEC	Cation Exchange Capacity
CI	Confidence Interval
CLD	Compact Letter Display
CTI	Composite Tolerance Index
DxM	*Populus deltoides* × *Populus maximowiczii*
DxN	*Populus deltoides* × *Populus nigra*
EMMs	Estimated Marginal Means
For	Forest land (continuous forest cover >100 years)
FSC	Forest Stewardship Council
GLMM	Generalized Linear Mixed Model
H^2	Broad-sense heritability
LM	Linear Model
LMM	Linear Mixed Model
MAI	Volumetric mean annual increment
$Mgha^{-1}$	Megagram per hectare (metric ton per hectare)
MxT	*Populus maximowiczii* × *Populus trichocarpa*
MV-LMM	Multivariate Linear Mixed Model
PC1	First Principal Component
PCA	Principal Component Analysis
PEFC	Programme for the Endorsement of Forest Certification
PRISMA	Preferred Reporting Items for Systematic Reviews and Meta-Analyses
SE	Standard Error
T	*Populus trichocarpa*
ZI-Gamma	Zero-inflated Gamma

1. Introduction

1.1 Ecology and global usage of *Populus* species

The genus *Populus* encompasses approximately 30 tree species widely distributed across the Northern Hemisphere, including Europe, Asia, and North America (Jobling 1990). These species are ecologically characterized by their fast growth, light-demanding nature, and ability to colonize disturbed or open habitats (Jobling 1990; Stettler *et al.* 1996; Isebrands & Richardson 2014). Most *Populus* species are early successional, exhibiting high photosynthetic rates and efficient nutrient uptake, which makes them well-adapted to short-rotation silvicultural systems (Jobling 1990; Stanturf *et al.* 2001). The genus includes three broadly recognized groups: aspens (e.g., *P. tremula*, *P. tremuloides*), cottonwoods or Aigeiros poplars (e.g., *P. deltoides*, *P. nigra*), and balsam or Tacamahaca poplars (e.g., *P. trichocarpa*, *P. balsamifera*, *P. maximowiczii*), along with their numerous interspecific hybrids.

Globally, *Populus* species are among the most widely cultivated trees for industrial and environmental purposes (Jobling 1990; Stanturf *et al.* 2001; Isebrands & Richardson 2014; Stanturf & Oosten 2014). Their uses span pulp and paper production, sawn timber, bioenergy, and ecosystem services, such as phytoremediation, floodplain restoration, and carbon sequestration (Dickmann 2006; Park & Wilson 2007; Dieter 2016). Intensive breeding programs have resulted in high-yielding hybrids, such as *P.* × *canadensis* (*P. deltoides* × *P. nigra*) and *P. trichocarpa* hybrids, which have been selected for their rapid growth, disease resistance, and suitability for diverse site conditions (Stanton *et al.* 2009; Biselli *et al.* 2022).

The largest *Populus* plantation-growing country is China, where over 7.5 million hectares are dedicated to poplar plantations for both timber and environmental services (Zili *et al.* 1999; Liu *et al.* 2025). In North America, *Populus* is widely present in natural systems, particularly in Canada (>30 million ha of natural stands, with *Populus* as the main species) and USA (>15 million ha of natural stands) (Ball *et al.* 2005). In several European countries, particularly France, Italy, and Spain, poplar is cultivated in intensive short-rotation systems on fertile agricultural land, using high-performance hybrids

under irrigation and fertilization to produce quality wood within 10–20 years (Chevallier 2000; Pra & Pettenella 2019; Oliveira *et al.* 2020). Poplar plantations in these regions often follow an agroforestry model or are integrated into agricultural landscapes, benefiting from fertile soils and mild climates (Schmutz 2017; Rosso *et al.* 2021; Thiesmeier 2024).
However, *Populus* cultivation remains relatively limited in Scandinavia. Native European aspen (*P. tremula* L.) is common in boreal forests but has limited commercial use because of browsing pressure, reduced disturbance regime and conifer-dominated forestry systems (Latva-Karjanmaa *et al.* 2007; Myking *et al.* 2011; Kusbach *et al.* 2024). Hybrid aspen (*Populus tremula* × *P. tremuloides* Michx.) is highly productive and has been planted in southern and central Sweden (Rytter & Stener 2005; Johansson 2013; Rytter & Stener 2014), but establishment is often constrained by heavy ungulate browsing, making fencing standard practice (Hjelm & Rytter 2016). Non-native poplar hybrids, particularly *Populus trichocarpa* Torr. & A.Gray ex Hook, *Populus maximowiczii* A.Henry, and their hybrids (hereafter referred to as poplars) show rapid growth on agricultural land but have demonstrated limited success on nutrient-poor or acidic forest soils (Böhlenius *et al.* 2018; Fahlvik & Böhlenius 2025; Muraro *et al.* 2025).
As the forest sector in Sweden seeks to diversify species composition under changing climate and certification demands, *Populus* species, particularly hybrids, are gaining interest as fast-growing alternatives to Norway spruce (*Picea abies* H. Karst) and Scots pine (*Pinus sylvestris* L.).

1.2 Role and potential of *Populus* in Swedish forestry

Swedish forestry has historically been, and still is today, dominated by coniferous species, particularly Norway spruce and Scots pine, which are well-adapted to northern boreal climates and have long supported the national forest industry (Skogsdata 2025). These monocultures are increasingly vulnerable to climate-related risks, pest outbreaks, and public scrutiny over ecological impacts (Felton *et al.* 2016; Gohli *et al.* 2024). Recent windthrow and bark beetle outbreaks, especially in the wake of storm Gudrun and similar disturbances, have exposed weaknesses in the resilience of spruce-dominated forests under a changing climate (Schlyter *et al.* 2006; Seidl & Rammer 2017; Müller *et al.* 2022).

Consequently, growing interest in climate-smart forestry, and diversification of wood production systems has driven attention toward fast-growing broadleaved alternatives, such as *Populus* species. These include native aspen, its hybrid with the American aspen *P. tremuloides* Michx (commonly referred to as hybrid aspen), and various interspecific poplar hybrids. In southern Sweden, where climatic conditions and longer growing seasons are favourable, these *Populus* taxa have demonstrated high productivity on fertile arable land, with yields reaching MAI up to 20-30 m^3 ha^{-1} yr^{-1} (Karacic *et al.* 2003; Christersson 2010; Rytter *et al.* 2016; Dimitriou & Mola-Yudego 2017; Karacic *et al.* 2021). Hybrid aspen and fast-growing poplars are currently commercially promising, given their rapid juvenile growth, short rotation potential, and suitability for pulp, energy, and timber production. Native aspen, while slower growing, is valued for its ecological role in promoting biodiversity and structural heterogeneity in mixed stands (Kouki *et al.* 2001; Mönkkönen *et al.* 2014; Caudullo *et al.* 2017), but commercial forestry using native aspen is currently non-existent (Edenius *et al.* 2011).

Despite their advantages, the use of *Populus* in operational forestry remains limited. Key concerns include high susceptibility to browsing by large herbivores (particularly in aspen and hybrid aspen), uncertainty regarding optimal silvicultural practices, and high establishment costs (Ostwald *et al.* 2013). Moreover, while private forest owners are interested in increasing productivity, they are often reluctant to adopt exotic tree species and more intensive management practices such as fertilization (Lindkvist *et al.* 2012; Hemström *et al.* 2014). This reluctance largely reflects limited knowledge about the economic, silvicultural, and environmental implications of hybrid *Populus* cultivation. Furthermore, poplar and hybrid aspen plantations in Sweden have historically been established on fertile, agricultural soils (Dimitriou & Mola-Yudego 2017; Mc Carthy *et al.* 2017; Lee *et al.* 2023), a limited and highly competitive land use (Slätmo 2019). This poses a major barrier to expansion.

In Sweden, an estimated 2.5 million hectares of forest land, and about 1.2 million hectares of forested arable land (former farmland afforested with spruce 50–70 years ago) could be available for establishing *Populus* plantations (Larsson *et al.* 2008; Böhlenius *et al.* 2023). Forested arable land is of particular interest: while it retains relatively high fertility and water-holding capacity, favourable for fast-growing broadleaves, it is often acidified after a full rotation (50–70 years) with Norway spruce (Hallbäcken & Tamm 2008; Thomaes *et al.* 2012). These conditions raise the question of whether *Populus* species can be successfully deployed beyond traditional high-fertility sites, provided that appropriate clone selection and site management are applied. Unlocking this potential requires a better understanding of how genotype, site type, and silvicultural treatments interact to influence establishment and early growth.

1.3 Establishment constraints for *Populus* species on forest land

The early establishment phase is critical to the success of fast-growing broadleaved species in production forestry. Among these, *Populus* species, particularly hybrid poplars, offer exceptional growth potential under suitable site conditions, but their adoption in Swedish forestry remains limited.

A key abiotic limitation for poplars is soil acidity, which is widespread in the podzolized, nutrient-poor forest soils of Sweden. Under low pH conditions, aluminium (Al^{3+}) becomes soluble and toxic, impairing root elongation, nutrient uptake, and overall plant vigor (Kisnerienė & Lapeikaitė 2015; Nogueirol *et al.* 2015). Poplars are particularly susceptible to aluminium stress (McCormick & Steiner 1978; Steiner *et al.* 1984; Timmer 1985). On acidic soils (pH < 5), significant reductions in root biomass, leaf area, and shoot height have been documented for many hybrid poplars(Naik *et al.* 2009; Smith *et al.* 2011; Böhlenius *et al.* 2016; Hjelm & Rytter 2016; Böhlenius *et al.* 2018). Nutrient availability, especially of calcium (Ca), magnesium (Mg), and phosphorus (P), is also a limiting factor on acid forest soils, where base cation depletion is common due to prolonged conifer dominance and leaching (Lundström 1993; Lundström *et al.* 2003; Prietzel & Stetter 2010). Root development and nutrient uptake in poplar species are strongly tied to soil base saturation and cation exchange capacity (CEC) (Fortier *et al.* 2015; Dhakad *et al.* 2025), which are often below critical thresholds for optimal growth on many podzolic forest sites (Chesworth 2007). This sensitivity reduces the number of sites suitable for deployment.

In contrast, European aspen and hybrid aspen generally exhibit greater tolerance to acidic conditions and Al toxicity (Böhlenius *et al.* 2018; Hjelm & Rytter 2018), likely due to their evolutionary adaptation to boreal environments. However, this advantage is offset by their vulnerability to browsing, particularly by moose (*Alces alces*) and roe deer (*Capreolus capreolus*), which often leads to severe damage or mortality during early stand development (Edenius *et al.* 2011; Bergqvist *et al.* 2014; Edenius & Ericsson 2015). In contrast, poplars tend to be less susceptible to ungulate browsing (Netzer 1984), which can reduce establishment losses; however, local pressure varies.

Competing vegetation is another major establishment challenge across *Populus* spp., with multiple studies showing that early weed control improves survival and growth in poplar and hybrid aspen plantings (Böhlenius & Övergaard 2015; Mc Carthy *et al.* 2017). The rapid colonization of clear-cuts by grasses and herbaceous vegetation can limit light, water, and nutrient availability to newly planted cuttings and seedlings (Davis *et al.* 1998; Coll *et al.* 2007). This is especially problematic for *Populus*, which require fast early growth to overcome their browsing and soil sensitivity.

Beyond biophysical constraints, operational deployment is also shaped by land-use competition and risk perceptions (see Section 1.2). While poplars have often been established on agricultural land (Christersson 2008; Stener & Westin 2017; Rytter & Lutter 2020), our focus here is the more abundant acidic forest and forested arable soils, which remain underutilized due to establishment failures, limited silvicultural guidance, and landowner perceptions (Lindkvist *et al.* 2012; Ostwald *et al.* 2013; Hemström *et al.* 2014). Moreover, non-native *Populus* species are subject to Swedish FSC/PEFC requirements (e.g., area limits, monitoring), which can restrict large-scale deployment for certified forest owners (FSC 2020; PEFC 2023).

Given this context, there is a pressing need to develop integrated strategies for improving poplar establishment on forest land. This includes identifying Al-tolerant genotypes, optimizing soil amendment treatments such as wood ash or lime to improve chemical properties (Arvidsson & Lundkvist 2003; Augusto *et al.* 2008; Arseneau *et al.* 2021), and refining site matching tools.

1.4 Addressing establishment constraints: potential solutions

Despite the recognized potential of *Populus* species in Swedish forestry, their deployment on forest soils remains limited. Addressing these constraints requires targeted silvicultural and genetic strategies that improve early survival and growth under operational conditions.

From a site preparation perspective, soil amendments offer a promising tool to alleviate abiotic limitations. Lime and wood ash raise pH and replenish base cations (Ca, Mg, K), thereby lowering Al^{3+} activity and improving nutrient availability (Derome 1990; Augusto *et al.* 2008; Reid & Watmough 2014; Ozyhar *et al.* 2022); biochar adds a slower, structural benefit by increasing water-holding capacity and cation-exchange capacity and can modestly buffer pH (Thomas & Gale 2015; Dai *et al.* 2017; Palviainen *et al.* 2020; Zhang *et al.* 2022). However, the effectiveness of these treatments for poplar species, and their interactions with different site types and application methods, remain poorly documented, especially for Swedish conditions.

At the same time, selecting the right planting material is critical for a successful establishment. Significant variation in abiotic stress tolerance exists among poplar clones, particularly in response to aluminium (Al) toxicity, a key factor limiting root development in acidic soils (Kochian *et al.* 2004; Hiradate *et al.* 2007). Systematic screening under controlled conditions allows the identification of genetically superior clones that combine vigor with enhanced stress tolerance.

Despite high potential, success on forest soils is uncertain due to acidity, Al toxicity, competing vegetation, browsing, and unclear clone × site × amendment guidelines under Swedish conditions. Evidence for performance on forested arable land remains fragmented. Operational prescriptions are also lacking.

This thesis explores both approaches: (1) evaluating the role of soil amendments to improve site conditions for poplar establishment on forest and forested arable land, and (2) identifying genetically tolerant clones through controlled screening and validation. Together, these strategies aim to reduce the establishment gap for *Populus* species in boreal forestry and support their integration beyond traditional farmland settings.

1.5 Thesis aims and research questions

The overarching aim of this thesis is to identify and evaluate practical strategies to improve the early establishment of poplars on acidic forest soils in Sweden. By integrating clonal selection, soil amendment testing, and field

validation, this work seeks to contribute to the development of fast-growing broadleaved species in boreal forestry.
More specifically, the thesis addresses the following research questions:

I. How does the establishment of poplars compare to other fast-growing broadleaved species and coniferous species on forest and forested arable land?
(Addressed in Chapter I)

II. What is the extent of genotypic variation in aluminium tolerance among poplar clones, and how can it be quantified?
(Addressed in Chapter II)

III. Can clonal differences in aluminium tolerance identified under controlled conditions be validated in acidic forest soils and forested arable land soils?
(Addressed in Chapter II)

IV. How do different soil amendments (wood ash, lime, and biochar) and application methods affect the establishment of poplars in acidic soil conditions?
(Addressed in Chapter III)

V. How does ash application influence the growth of poplars and other broadleaved tree species according to the scientific literature?
(Synthesized in Chapter IV)

The thesis takes a stepwise approach, beginning with broad species comparisons in operational field settings, then narrowing to clone-level physiological responses, and finally integrating both experimental data and literature evidence for future poplars deployment in Sweden.

2. Material and methods

This section provides the methodology used in each paper in the thesis. Each chapter applies a distinct methodological approach:

- Chapter I evaluates early survival and growth of hybrid poplar, hybrid aspen, birch, aspen, spruce and pine in field trials across seven sites representing forest land and forested arable land.
- Chapter II performs a greenhouse screening to assess aluminium tolerance in 70 hybrid poplar clones. Morphological and physiological traits were measured across increasing Al concentrations to estimate genotypic variation.
- Chapter III tests the effects of three soil amendments (wood ash, lime, biochar) on the field performance of hybrid poplar on acidic forest land and forested arable land.
- Chapter IV conducts a systematic literature review on the effects of wood ash on the growth of broadleaved temperate species.

2.1 Field sites

Both Chapter I and III are based on seven field experiments established in 2019–2020 in southern Sweden (Figure 1). Two contrasting site types were included: (i) forest land (For), with continuous forest cover for >100 years, and (ii) forested arable land (ArFor), i.e. former agricultural land afforested with Norway spruce for one rotation (≈40–70 years). In several cases, paired sites (e.g., For1/For2, ArFor1/For3, ArFor2/For4) were located within ~1 km to minimize climatic and edaphic variation between site types. Local weather data, including temperature and precipitation, were collected from nearby stations (within 10 km) to characterize site-level climatic conditions

All areas were newly clear-felled prior to establishment and mechanically prepared in rows using an excavator. To mitigate browsing, each site was fenced. Within sites, six 18 × 18 m plots were laid out, each assigned to one focal species (European aspen, hybrid aspen, silver birch [*Betula pendula* Roth], Scots pine, Norway spruce, or hybrid poplar). Planting was manual and followed the row preparation.

For site characterization, soil was sampled to 30 cm depth (12 samples per site; two per plot) and pooled to one composite per site for chemical analyses. Competing vegetation was quantified as a proxy for competition pressure using one 0.5 × 0.5 m clip frame per plot; samples were oven-dried and weighed. Plot-level species/treatment details (including poplar ash split-plots in Chapter I and amendment treatments in Chapter III) are described in the respective chapter-specific subsections.

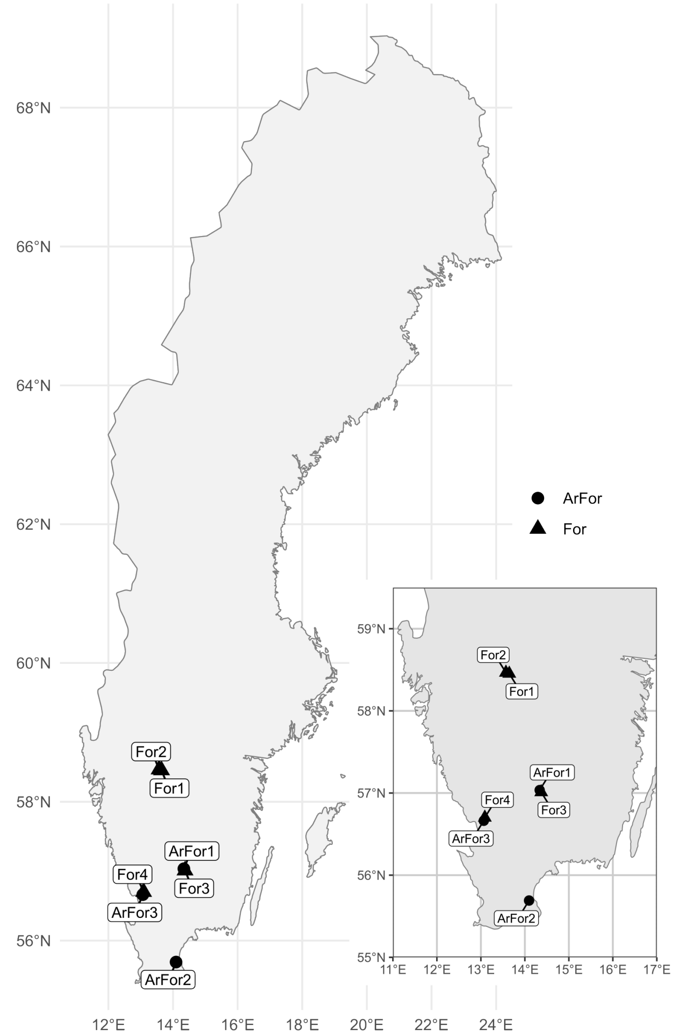

Figure 1. Overview map of Sweden and zoomed in Southern Sweden with experimental site locations. Two site categories were used: ArFor (former agricultural land converted to Norway spruce for 40–70 years) and For (areas with continuous forest cover exceeding a century). Site pairs in close proximity

(For1/For2, ArFor1/For3, ArFor2/For4) are within ~1 km and therefore appear as a single symbol on the map.

2.2 Chapter I – Multi-species field comparison across site types

This chapter is based on a multi-site field experiment designed to assess early establishment performance of six tree species across two contrasting site types in southern Sweden under operational planting conditions.

The study took place at the field sites described in section 2.1. At each site, six plots (18 × 18 m) were established, each assigned to one species: European aspen, hybrid aspen, silver birch, Scots pine, Norway spruce, or hybrid poplar (hereafter "poplars"). All species except poplar were planted at 3 × 1.5 m spacing with 50 containerized seedlings per plot. For poplar, a split-plot design was implemented: within each poplar plot, 25 planting positions received wood ash at 3 Mg ha^{-1} mixed into the planting spot prior to planting (Poplar AT), and 10 positions remained untreated (Poplar UT). All planting was done manually following mechanical row preparation.

Planting stock represented the best available genetic material. European aspen clones 14, 34, 45, 47, 51, 76 were selected from the Swedish Aspen (SwAsp) program (Luquez *et al.* 2008) and hybrid aspen clones SK884012 and SK884015 were sourced from a commercial nursery (Sydplantor, Tingsryd, Sweden). Birch (Ekebo 5), Norway spruce (Elite35+), and Scots pine (Gottardberg särplock) containerized seedlings were obtained from Södra Odlarna (Falkenberg, Sweden).

Poplar seedlings were produced from dormant cuttings collected in February 2019 and stored at 4 °C until April the same year. Cuttings were potted into 250 mL containers filled with a nursery mix (83% peat, 5% clay, 7% gravel, 5% hydrograins) and grown under field conditions until reaching approximately 40 cm in height and 4 mm in root-collar diameter. All planting stock was stored at +2 °C before field planting in spring 2020. Average seedling height at planting was ~40 cm for aspen and hybrid aspen, ~50 cm for birch, ~30 cm for Scots pine, ~35 cm for Norway spruce, and ~40 cm for poplar.

Wood ash used in Poplar AT treatments consisted of 95% bottom ash and 5% fly ash derived from forest-biomass combustion. Ash samples were analyzed (Chapter I—S1).

Plant survival and height were recorded at planting and annually for three years. To assess soil chemical properties, 12 soil samples per site (two per plot) were collected at 30 cm depth and pooled to generate one composite sample per site. Soil analyses were conducted by Eurofins Agro Testing Sweden AB (Kristianstad, Sweden).

Vegetation biomass was assessed as a proxy for competitive pressure. One sample per plot (six per site) was collected using a 0.5 × 0.5 m frame; samples were oven-dried and weighed to quantify aboveground competing vegetation (Chapter I - Table 2).

2.3 Chapter II – Aluminium tolerance screening and soil validation

This chapter is based on two controlled-environment experiments designed to evaluate aluminium (Al) tolerance in hybrid poplar clones. The first experiment involved a large-scale screening of clonal variation under standardized Al stress conditions. The second experiment validated clone performance in contrasting soil types to assess genotype-by-environment interactions related to Al sensitivity. Seventy poplar (*Populus* spp.) clones representing a broad range of hybrid pedigrees were selected from Swedish clonal archives (Chapter II - Table S1). The cross types selected were *P. deltoides* × *P. maximowiczii* (DxM), *P. nigra* × *P. maximowiczii* (NxM), *P. maximowiczii* × *P. trichocarpa* (MxT), *P. deltoides* × *P. nigra* (DxN), and intraspecific *P. trichocarpa* crosses (T).

In the first experiment, cuttings were planted in 450 mL pots filled with washed siliceous quartz sand (grain size 0.45 mm; Baskarpssand AB, Habo, Sweden) and grown in a greenhouse under controlled conditions (20 °C, 20-hour photoperiod). Supplemental fluorescent lighting provided a total photon flux density of 130 µmol m^{-2} s^{-1}. During the three-week pre-cultivation phase, plants were irrigated with a nutrient solution consisting of 0.37 g L^{-1} Superba Röd and 0.37 g L^{-1} Calcinit YARA Liva, with solution pH adjusted to 4.2 using HCl.

After pre-cultivation, plants were exposed to four aluminium treatments (0, 100, 150, 200 mg L^{-1} Al^{3+}) applied via irrigation with aluminium chloride ($AlCl_3$). The treatment solution pH was maintained at 4.2 using HCl or NaOH. Plants were arranged in a randomized complete block design with six blocks, each containing one plant per clone for each Al treatment level. After

six weeks of exposure, final plant height (H_{fin}) was measured, and plants were harvested. Root systems were carefully washed, dried at 70 °C for 48 h, and weighed to determine root biomass (R_{fin})
The second experiment assessed the performance of four selected clones in contrasting acidic soil types: (i) boreal forest soil and (ii) forested arable land soil. Soil samples were analyzed by Eurofins Agro Testing Sweden AB (Kristianstad, Sweden) (Table 1). Dormant cuttings were rooted in 250 mL containers filled with a nursery substrate composed of 83% peat, 5% clay, 7% gravel, 7% hydrograins, enriched with N–P–K (11–5–8) fertilizer and micronutrients, and adjusted to pH 5.5–6.5. Plants were grown under the same greenhouse conditions as in Experiment 1 until they reached ~40 cm in height and ~5 mm stem diameter.
Subsequently, plants were transplanted into 3 L pots filled with either forest or forested-arable soil. The experiment followed a randomized complete block design with six blocks, each containing one plant per clone–soil combination. Plant height was measured every 10 days over 50 days (five time points). At harvest, shoots and roots were separated, oven-dried at 70 °C for 48 h, and weighed. In addition, the area of the first fully developed leaf was measured by scanning with a flatbed scanner and analyzed using ImageJ (Schneider et al., 2012).

2.4 Chapter III – Soil amendment effect on the early growth of poplars in acidic soils

This chapter is designed to evaluate the effect of soil amendments (wood ash, lime, and biochar) on the early establishment and growth of poplar clones under contrasting soil conditions. The experiment aimed to test whether targeted amendments could mitigate establishment barriers on acidic, nutrient-depleted forest soils, thereby supporting broader deployment of poplars on non-agricultural land. The study took place at the field sites described in section 2.1.
Dormant cuttings of selected poplar clones were collected in February 2019, stored at 4 °C, and pre-cultivated in containers filled with a nursery substrate in April. After one season of growth under field conditions, the one-year-old plants were stored at +2 °C during winter and outplanted in spring 2020. All sites were mechanically prepared in rows using an excavator and enclosed with fencing to prevent browsing.

The trial included seven sites in total (For1–3 and ArFor1–4) and involved two distinct clone sets. At five of the sites, four commercially available clones were used: ‘Androscoggin’, ‘Rochester’, clone ‘14’, and ‘OP42’, representing various combinations of *P. trichocarpa*, *P. maximowiczii*, and *P. nigra*. At the remaining three sites, four SnowTiger® SLU clones (‘23.4’, ‘26.1’, ‘44.7’, and ‘722.16’) were tested; these were intra-specific hybrids of *P. trichocarpa*. All clones are referred to as "poplar" in the context of this study.

At each site, plants were established in plots treated with either (i) wood ash (3 Mg ha^{-1}), (ii) lime (3 Mg ha^{-1}), or (iii) biochar (20 Mg ha^{-1}), as well as an untreated control. Within each treatment plot, four application methods were implemented: (a) Mixed, where the amendment was incorporated into the top 30 cm of a 1 × 1 m square; (b) Surface, where it was spread evenly on the surface within the same area; (c) Spot, where it was applied in a 0.3 m diameter planting hole; and (d) Control, where no amendment was used. Subplots representing each method were randomly distributed, and spacing between plants was 1.5 × 3 m (Chapter III - Figure 1). Within each amendment type, 25 plants received the Mix treatment, and 10 each were assigned to the Surface, Spot, and Control subplots. Clone identity and distribution within plots followed a standardized allocation protocol.

The amendments used were representative of operationally relevant materials. Pulverized calcitic lime (particle size 0–0.02 mm) was supplied by Nordkalk AB (Ingaberga, Sweden). Biochar was produced by pyrolysis (750 °C) of barley and wheat seed residues in a Pyreg® unit, yielding 4 × 20 mm pellets. Wood ash was derived from the combustion of coniferous forest residues (95% bottom ash, 5% fly ash) in a commercial biomass boiler. Chemical properties of the amendments were analyzed at certified laboratories using standardized digestion and quantification procedures (Chapter III - Table 2).

Tree survival, height, and root collar diameter were recorded at planting and after the first, second, and third growing seasons. To assess the effects of treatments on soil chemical properties, twelve soil samples were collected from each site in year three, specifically from Mixed-treated plots and untreated controls. Samples were taken from a depth of 0–30 cm and pooled by treatment within each site. Analyses were conducted at Eurofins Agro Testing Sweden AB using the AL (Ammonium Lactate) method and inductively coupled plasma optical emission spectrometry to determine macro- and micronutrient concentrations (Chapter III - Table 3).

2.5 Chapter IV– Systematic review on the growth effect of ash application on broadleaved trees

This chapter builds upon a systematic review conducted to assess the growth effects of wood ash application on temperate and boreal broadleaved tree species. The review aimed to synthesize experimental findings across diverse environments and study designs to evaluate whether wood ash, as a silvicultural amendment, consistently improves broadleaved tree growth. The review also sought to contextualize and support the field trials described in Chapter III.

Following a structured literature search and screening process (Figure 2), 41 peer-reviewed articles published between 1988 and 2025 were selected for inclusion. The reviewed studies originated predominantly from northern and central Europe, including Finland, Sweden, Estonia, Germany, and the United Kingdom, but also included work from North America and East Asia. No geographic or publication-year restrictions were imposed in the search stage, and the scope was limited to broadleaved species used in temperate or boreal ecosystems.

To be included, studies had to meet three criteria: (i) the species studied were broadleaved trees compatible with temperate or boreal forestry conditions, (ii) wood ash was purposefully applied in known quantities, and (iii) growth-related parameters such as survival, height, diameter, or biomass were reported. Studies that focused exclusively on coniferous species, tropical species, or phytoremediation of polluted sites without silvicultural context were excluded. Furthermore, only studies published in English and accessible in full text were included (Figure 2).

For each study, detailed data were extracted regarding site characteristics, species identity, age or developmental stage of the trees, ash type and dosage, application method, and the soil type (e.g., mineral, organic, degraded peat). Both field and greenhouse experiments were included, provided that a direct comparison could be made between ash-treated and untreated controls or relevant alternatives. Ash treatments co-applied with nitrogen fertilizer were only included if the experimental design also incorporated nitrogen-only controls, thereby allowing the ash effect to be isolated.

The extracted dataset covered several categories of information. First, site and species details were recorded, including geographic location, taxonomic identity, hybrid status, and age class of the trees. Second, ash properties were noted, such as origin (biomass source), type (bottom ash, fly ash, or mixed), application rate (e.g., Mg ha^{-1} or g pot^{-1}), and chemical composition when available. Third, soil type was classified, with particular attention to differences between organic and mineral soils. In addition, growth parameters such as height, diameter, basal area, and above- or belowground biomass were extracted. Finally, the experimental setting was described, distinguishing between greenhouse/pot experiments and field trials. The final dataset included several cases where multiple studies were conducted on the same site or experimental platform but reported different growth parameters, time points, or species-specific effects. For instance, studies by Hytönen and Kaunisto (1999) and Hytönen and Aro (2012) were treated as separate entries, as they examined different aspects of growth response to ash on a shared site. We quantified ash effects by extracting published data and expressing responses as percent change relative to the control (0% = neutral). Positive effects were classified as + (0–30%), ++ (>30–50%), and +++ (>50%), and negative effects as – (0–30%), – – (>30–50%), and – – – (>50%).

Although meta-analysis was not performed due to heterogeneity in experimental designs, reporting formats, and units, the data were organized to enable qualitative synthesis and identification of trends across species, ash dosages, and soil types. Where possible, ash effects were interpreted in relation to application rate, base saturation improvement, and pH change. These patterns were then discussed in the light of silvicultural potential, particularly for *Populus* species and other fast-growing broadleaves under Swedish forest conditions.

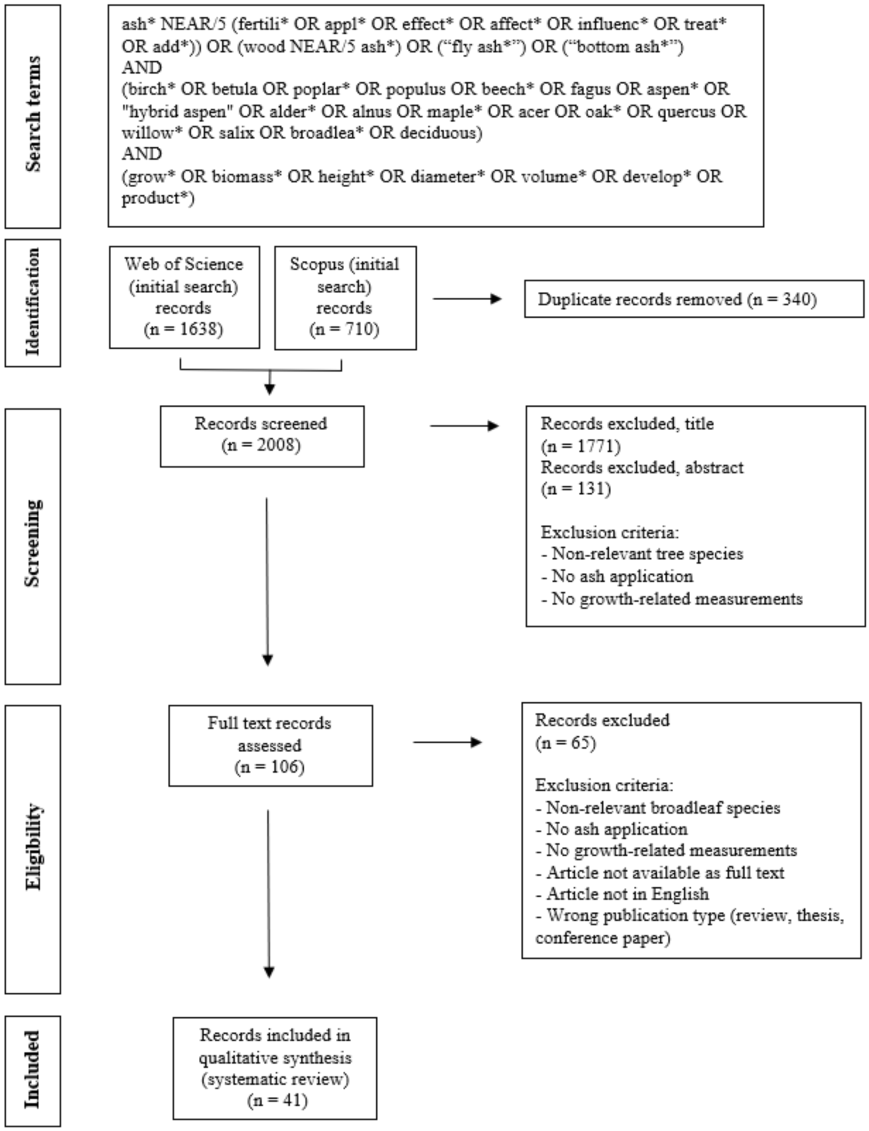

Figure 2. A flow diagram describing the systematic review process adapted from PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) 2020.

2.6 Statistical analyses

This section presents the statistical analyses conducted for Chapters I, II, and III. In contrast, no statistical analyses were performed in Chapter IV, as it was based on a systematic review approach focused on the qualitative synthesis of existing literature. In chapters I and II all the analyses were performed in R version 4.5.1 (R Core Team 2025) using RStudio 2025.05.1+513 (Posit Team 2025). Chapter III analyses were performed in R version 4.4.1 (R Core Team 2024). All figures and visualizations were produced using the ggplot2 package (Wickham 2016) and ggh4x (van den Brand 2023).

2.6.1 Chapter I

To assess differences in early establishment among tree species across site types, we analyzed survival, growth, and overall performance using a combination of generalized linear mixed models (GLMMs), linear models (LMs), and multivariate analysis.

Survival (binary response) was analyzed using GLMMs with a binomial distribution, implemented in the glmmTMB package (Brooks *et al.* 2017). Tree growth across years (height and root collar diameter) was analyzed using a zero-inflated Gamma (ZI-Gamma) GLMM, also via glmmTMB, to account for excess zeros. Fixed effects included site type (For, ArFor), species, year, and their interactions. A log link was specified for the conditional component, and a constant intercept was assumed in the zero-inflation model (ziformula = ~1).

Final tree height was also analyzed separately using linear models (LMs), with species, site type, and their interaction as fixed effects. Significance testing for all fixed effects was based on Type III Wald χ^2 tests using the Anova() function in the car package (Fox & Weisberg 2018). Pairwise comparisons were conducted using Tukey's HSD via the emmeans package (Lenth 2023), with a significance threshold of $p \leq 0.05$. Model residuals were inspected using the DHARMa package (Hartig 2022) to confirm normality and absence of influential outliers.

To evaluate species establishment performance, a Principal Component Analysis (PCA) was conducted on height (gh1, gh2, gh3), diameter growth (gd1, gd2, gd3), and survival in year 3 (s3). The first principal component (PC1) scores, representing overall establishment success, were analyzed using an LM with species, site type, and their interaction as fixed effects.

Full model outputs are available in the supplementary materials (Chapter I-S2-S6).

2.6.2 Chapter II

Height and root biomass were jointly analyzed using a multivariate linear mixed model (MV-LMM) implemented via the mmer function in the sommer package (Covarrubias-Pazaran 2016). The model included aluminium concentration (dose), species, and their interaction as fixed effects, and clone and block as random effects:

$$\begin{bmatrix} H_{fin} \\ R_{fin} \end{bmatrix} = X\beta + Z_c u_c + Z_b u_b + \varepsilon$$

Where $\begin{bmatrix} H_{fin} \\ R_{fin} \end{bmatrix}$ are the response variables final height and root biomass, $X\beta$ represents the fixed effects of aluminium concentration (dose), species, and their interaction, $Z_c u_c$ random clone effects, $Z_b u_b$ random block effect and ε is the residual error. An unstructured covariance matrix was used for the random effects to allow estimation of genetic correlations across traits. Broad-sense heritability (H^2) was calculated as:

$$H^2 = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_B^2 + \sigma_E^2}$$

where σ_G^2 is the genetic variance among clones, σ_B^2 the block variance, and σ_E^2 the residual variance (Piepho *et al.* 2008). The genetic correlation between final height (H_{fin}) and root biomass (R_{fin}) was calculated from the G-matrix as:

$$r_g = \frac{\sigma_G(H_{fin}, R_{fin})}{\sqrt{\sigma_G(H_{fin})\,\sigma_G(R_{fin})}}$$

Here, $\sigma_G(H_{fin}, R_{fin})$ is the genetic covariance between the two traits, and $\sigma_G(H_{fin})$ and $var_G(R_{fin})$ are their genetic variances.

Best Linear Unbiased Predictions (BLUPs) were extracted to estimate clone-specific performance.

For each clone, trait values across aluminium treatments were normalized against the control (0 mg L^{-1} Al) to compute relative growth indices. The area under the relative growth curve (AUC) was calculated using trapezoidal numerical integration (pracma::trapz) (Borchers 2019) to summarize aluminium tolerance per clone. The AUC and BLUP scores were z-standardized and summed to derive a Composite Tolerance Index (CTI), representing both genetic merit and phenotypic plasticity under aluminium stress.

To evaluate dose-response curves for final height, quadratic regression models were fitted for each clone individually:

$$h_{\text{final}} = \beta_0 + \beta_1 \times \text{conc} + \beta_2 \times conc^2 + \varepsilon$$

where h_{final} is the final height, *conc* is the aluminium concentration (0, 100, 150 and 200 mg L^{-1}), β_0 is the intercept, β_1 and β_2 are the regression coefficients and ε is the error term. Model fit was assessed using R^2, and 95% confidence intervals were computed.

For the validation experiment, growth over time (height and diameter) was analyzed using linear mixed-effects models (LMMs) with the lme4 package (Bates *et al.* 2015). Fixed effects included time (five intervals), clone, soil type, and their interactions. Block was treated as a random effect to account for spatial heterogeneity:

$$y_{ijkl} = \mu + \text{time}_i + \text{clone}_j + \text{soil}_k + (\text{time} \times \text{clone} \times \text{soil})_{ijk} + b_l + \varepsilon_{ijkl}$$

where y_{ijkl} denotes the observed response for the j-th clone, in soil type k, within block l, at time interval i. The model included time (five intervals, recorded every 10 days), clone (selected based on prior screening performance), and soil type (two treatments) as fixed effects, along with their interactions. Block (b_l) was included as a random effect to account for spatial heterogeneity among the six blocks. The residual error term ε_{ijkl} captures the unexplained variation.

Final traits (root biomass, shoot biomass, leaf area, shoot:root ratio) were analyzed via linear models with clone, soil, and their interaction as fixed effects, and block as a covariate. Type III ANOVAs were conducted using car::Anova() (Fox & Weisberg 2018), with post-hoc comparisons via the emmeans package (Lenth 2023). Group differences were visualized with compact letter displays (CLDs) (Lenth 2016).

2.6.3 Chapter III

To assess treatment effects on early tree performance, we evaluated tree height, root collar diameter, and survival across different soil amendments (wood ash, lime, biochar) and application methods (Mixed, Surface, Spot, and Untreated). Tree height and diameter were analyzed using linear mixed-effects models (LMMs) fitted with the lme4 package (Bates *et al.* 2015). Survival was modeled as a binary response using generalized linear mixed-effects models (GLMMs) with a binomial distribution, implemented via the glmmTMB package (Brooks *et al.* 2017).

For all models, fixed effects included: site type (For, ArFor), amendment type (ash, lime, biochar), application method (Mixed, Surface, Spot, Untreated) and their interactions. Site was included as a random effect. Post-hoc pairwise comparisons were conducted using Tukey's HSD tests with the emmeans package (Lenth 2023), with significance assessed at $p \leq 0.05$. Residual diagnostics, including assessment of distribution, homoscedasticity, and influential points, were performed using the DHARMa package (Hartig 2022), confirming assumptions of model validity.

To further investigate treatment efficacy under the Mixed application method, we tested whether soil chemical characteristics (pH, total N, available P, exchangeable K, Al, Ca, and Mg) were associated with tree height after three growing seasons. This analysis was conducted using multiple linear regression models. Supplementary tables include model summaries, effect estimates, and residual diagnostics.

3. Results and discussion

3.1 Species–site matchmaking: lessons from early establishment (Chapter I)

Our findings show that early establishment is strongly governed by species × site interactions, with implications for operational forestry and for diversification under a changing climate (Felton *et al.* 2016; Jactel *et al.* 2018; Pukkala 2018; Pardos *et al.* 2021). Survival on Forest Land (For) was generally high for most species (≈90% by year 3), whereas Forested Arable Land (ArFor) produced more variable outcomes. Conifers, Norway spruce (≈30% ± 7%) and Scots pine (≈55% ± 8%), suffered high mortality on ArFor (Figure 3A), consistent with lower early competitive ability where dense, nutrient-demanding vegetation develops on fertile substrates (Grubb 1977; Jylhä & Hytönen 2006). In contrast, pioneer broadleaves such as silver birch, European aspen, and wood-ash-treated poplar (Poplar AT) were more competitive in these environments and frequently overtopped the ground vegetation in the first years after planting (Whitmore 1989; Dalling & Hubbell 2002).

Growth responses reinforced these contrasts. Hybrid aspen and birch displayed the strongest height growth on For (Figure 3B), where competition pressure was lower and the acidic, nutrient-poorer soils nonetheless suit these taxa (Ericsson & Lindsjö 1981; Hynynen *et al.* 2010; Rytter & Stener 2014). Poplar AT performed best on ArFor, where ash likely raised pH and replenished base cations; untreated poplar (Poplar UT) grew poorly across both site types, consistent with poplar requirement for pH > 5.5 and higher base saturation (Bergstedt 1981; Jobling 1990; Thomaes *et al.* 2012; Hjelm & Rytter 2016). Quantitatively, Poplar AT reached a median height of ~250 cm on ArFor compared with ~220 cm on For, while soils across trials were acidic (pH ≈ 4.1–5.2), explaining the weak response of Poplar UT. These findings align with studies showing that wood ash on acid forest soils can improve nutrient availability and poplar growth (Bona *et al.* 2008; Arseneau *et al.* 2021; Muraro *et al.* 2025).

The multivariate summary corroborated these patterns. Principal component analysis (PC1 explained >70% of variance) separated species by establishment success (Figure 4). Hybrid aspen, birch, European aspen, Scots pine, and Norway spruce scored higher on For than on ArFor, reflecting more reliable establishment where competition was reduced. By contrast, Poplar AT, Poplar UT, and, European aspen showed no significant differences between site types, suggesting broader deployment potential under appropriate management. Importantly, the PC1 patterns indicate that high fertility on ArFor does not guarantee successful establishment: without intervention, vigorous understory vegetation can negate any growth advantage of fertile soils (Grubb 1977; Jylhä & Hytönen 2006).

In line with previous work, hybrid aspen combined rapid early height growth with high survival in our trials, extending evidence for strong establishment beyond traditional arable contexts (Johansson 2013; Rytter & Stener 2014; Rytter & Lutter 2020). Silver birch likewise showed robust survival (≈80%) and better height growth on For than on ArFor (mean growth ~75 cm vs. ~30 cm by year 3; Figure 3B), matching its adaptation to nutrient-poor, acidic forest soils (Hynynen *et al.* 2010) and recent breeding advancements that have increased MAI on suitable sites (Liziniewicz *et al.* 2022). European aspen displayed high site adaptability with median heights around 150 cm and similar survival across site types, a result consistent with its broad ecological amplitude and biodiversity value despite historically modest interest in commercial deployment (Kouki *et al.* 2001; Edenius *et al.* 2011; Mönkkönen *et al.* 2014; Caudullo *et al.* 2017; Kusbach *et al.* 2024). The productivity gap between unimproved aspen and hybrid aspen is well documented (Yu *et al.* 2001; Lutter *et al.* 2017) but could be narrowed through clonal selection and breeding targeting survival, growth, and browsing/pest tolerance (Ruotsalainen 2014; Jansson *et al.* 2017). Although breeding cycles in trees are long (Grattapaglia 2017; Lebedev *et al.* 2020), genomic selection and biotechnology offer possibilities to accelerate delivery of improved material (Ahmar *et al.* 2021; Grattapaglia 2022).

Beyond pure stands, early-rotation results support using fast-growing broadleaves as nurse crops to facilitate the establishment of shade-tolerant conifers. On forest sites in northern Europe, birch has a long record as a shelter species for Norway spruce, with positive outcomes for microclimate and stand development (Mård 1996; Valkonen & Valsta 2001; Frivold & Frank 2002; Saccone *et al.* 2009; Lundqvist *et al.* 2014). The nurse-species role of hybrid aspen remains comparatively underexplored in Fennoscandia, yet analogous systems with trembling aspen (*Populus tremuloides* Michx) and planted white spruce (*Picea glauca* (Moench) in Canada have shown facilitative effects and operational feasibility (Pitt *et al.* 2015; Kabzems *et al.* 2016; Lieffers *et al.* 2018). On ArFor, hybrid poplar can serve as a short-rotation nurse crop that also provides early biomass. After thinning or final felling, the released growing space can be utilized by an understory shade-tolerant species. This approach is consistent with previous studies showing that poplar can moderate microclimate and suppress competing vegetation, thereby creating favorable conditions for the succeeding crop species (Josiah & Kuhn 2000; Nelson *et al.* 2012; Boothroyd-Roberts *et al.* 2013; Stark *et al.* 2015; Bouchard *et al.* 2018).

All these options must nevertheless be considered within certification frameworks, as in Sweden, a large share of productive forest (~65%) is certified (Skogsdata 2025). FSC typically restricts non-native species to ≤ 5% of productive area and PEFC to ≤ 20% for large owners (FSC 2020; PEFC 2023). Nonetheless, current plantings of hybrid aspen and poplar remain well below 10,000 ha (Mc Carthy 2016), indicating scope for expansion within existing limits; and because Norway spruce is classified as non-native in Skåne, replacing it with other non-natives (e.g., poplar) can be certification-compliant in that region.

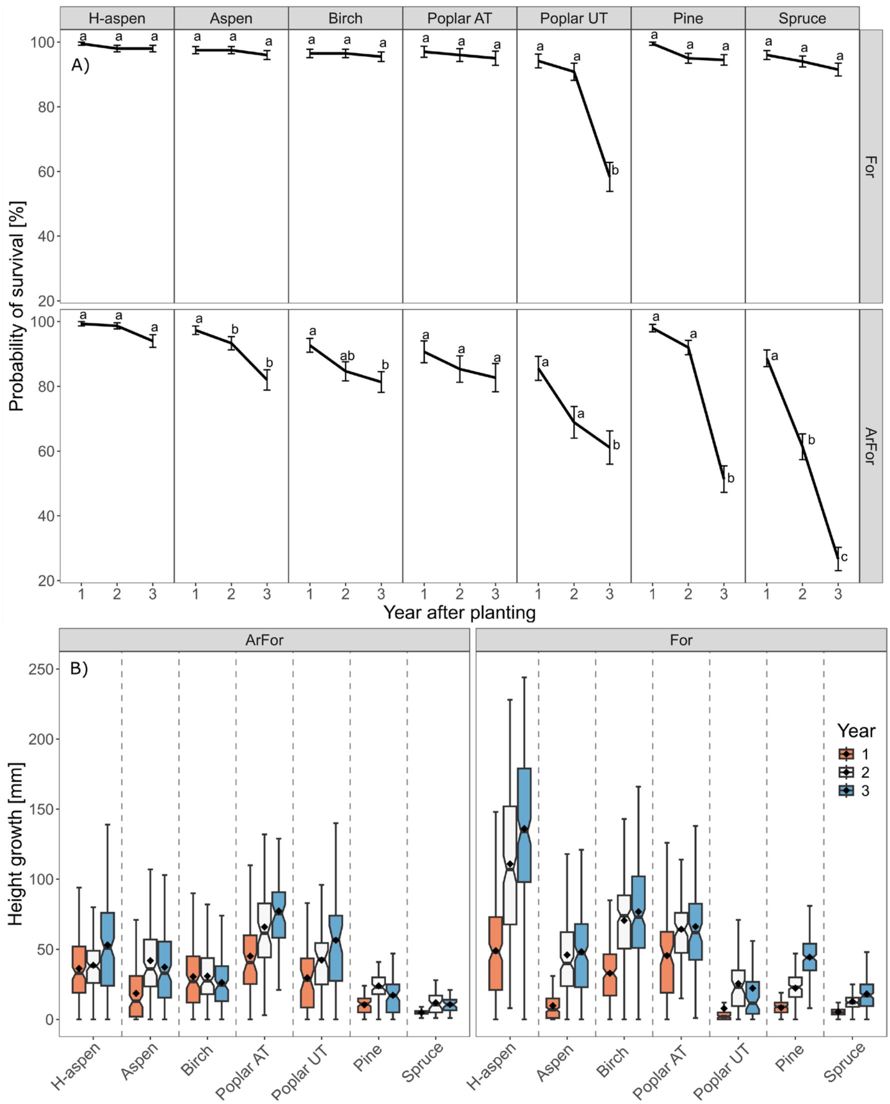

Figure 3. A) Survival probability (mean estimates ± SE) of six tree species: hybrid aspen, European aspen, silver birch, poplar with ash treatment (Poplar AT), untreated poplar (Poplar UT), Scots pine, and Norway spruce on Forest Land (For) and Forested Arable Land (ArFor) during the first three years after planting. Separate panels illustrate each species. Survival is shown as a function of establishment year. Vertical bars represent standard errors, and different letters denote significant differences between years within the same species and site type ($p<0.05$). B) Box plots showing mean annual growth distributions (cm) of six tree species (hybrid

aspen, aspen, birch, poplar AT, poplar UT, pine, spruce) in ArFor and For during three years after planting. Each box represents the interquartile range, the line inside the box indicates the median, with whiskers extending to the distribution range. Dots represent the mean height for the species at the particular year. Colors correspond to different growing seasons after planting, with red representing the first year, white the second and dark blue representing year three.

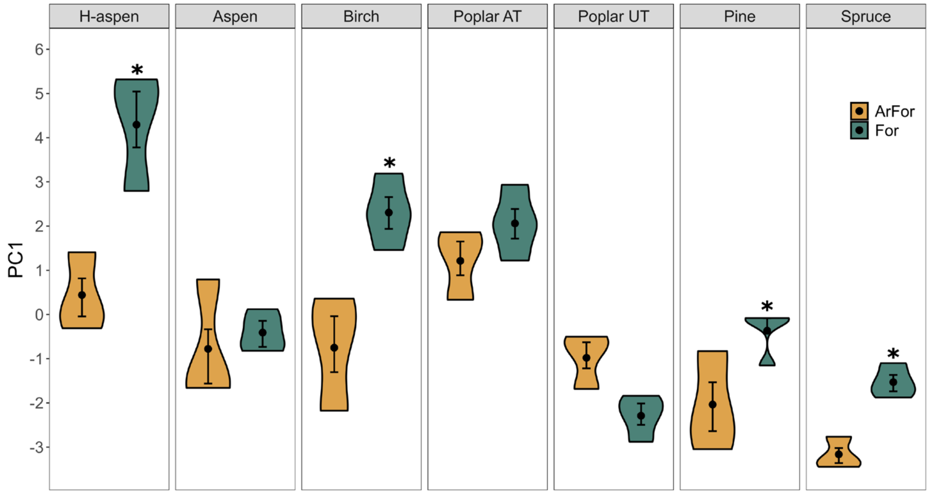

Figure 4. Violin graph showing PC1 scores from principal component analysis for six tree species (hybrid aspen, aspen, birch, poplar AT, poplar UT, pine, spruce) in Forested Arable Land (ArFor, orange) and Forest Land (For, green). Each panel represents a different species. Asterisks denote statistically significant differences ($p<0.05$) between land types within each tree species. Bars represent interquartile variation.

3.1.1 Strategic outlook of forest diversification with fast-growing species in Sweden

The results from this study underline that diversification with *Populus* and other fast-growing broadleaves must be grounded in site-specific deployment strategies that combine species-site matching with targeted interventions.

On forest land (For), high survival and strong early growth of hybrid aspen and birch make them attractive diversification candidates, capable of delivering shorter rotations, earlier economic returns, and enhanced carbon sequestration (Rytter & Stener 2005; Uri *et al.* 2012; Rytter & Stener 2014; Dubois *et al.* 2020; Lutter *et al.* 2024). On forested arable land (ArFor), poplars combined with wood ash emerge as a viable option, but long-term studies to confirm the feasibility are needed.

Mixed-species systems can offer further opportunities. Birch and hybrid aspen can serve as nurse crops for shade-tolerant conifers such as spruce in forest land (Frivold & Frank 2002; Saccone *et al.* 2009), while in forested arable land, poplar could function as a short-rotation nurse for high-value species, providing early income while preparing the site for a second crop tree. These approaches align with diversification goals while spreading risk across species with differing vulnerabilities to pests, pathogens, and climatic extremes (Felton *et al.* 2016; Bauhus *et al.* 2017).

Operational decisions must also consider cost-effectiveness. On fertile sites with intense vegetation competition, repeated control could sustain conifers, but the costs may outweigh returns. Browsing pressure, while not addressed in this trial, remains a potential constraint on broadleaf deployment in operational settings, requiring site-by-site assessment.

Regulatory frameworks set limits [FSC (≤ 5%) and PEFC (≤ 20%)] for non-native species, but current *Populus* and hybrid aspen planting levels are far below these thresholds. This leaves scope for strategic expansion without breaching certification standards, particularly on site types identified here as high potential.

Looking forward, climate change adds both urgency and complexity. Warmer, drier summers may disadvantage shallow-rooted species on light soils while favouring drought-tolerant genotypes and shifts in pest dynamics could alter species performance over time (Li *et al.* 2024; Wang *et al.* 2024). In this context, *Populus* species could be deployed as part of a risk-management strategy, alongside other broadleaves, rather than as a single-species alternative to conifers.

Importantly, long-term monitoring is essential to confirm whether the early establishment patterns documented here persist over full rotations and under variable climatic conditions. Genetic improvement remains an underexploited lever for adaptation: breeding programs could target multi-trait resilience, combining drought, pest, and browsing resistance. Modern breeding tools, including genomic selection and vegetative propagation, could shorten the selection cycle for tree species to one or two decades (Grattapaglia *et al.* 2018; Ahmar *et al.* 2021), delivering site-adapted, high-performing material to meet both productivity and resilience goals.

3.2 Poplars can be screened and selected for aluminium tolerance (Chapter II)

We evaluated aluminium (Al) tolerance in 70 poplar (*Populus* spp.) clones using a two-phase approach: a screening under controlled greenhouse conditions, followed by a soil validation experiment under two contrasting site types, forested arable and forest soils. This approach enabled us to quantify genetic variation, estimate heritability, identify tolerant and susceptible clones, and test whether performance under controlled conditions translated into acidic soil conditions.

Al concentration significantly reduced both height and root biomass ($p < 0.001$). Compared with the control, height decreased by 22.7, 26.4, and 31.2 cm at 100, 150, and 200 mg L^{-1} Al, respectively, root biomass decreased by 0.78, 0.98, and 1.03 g at the same doses. Clear species-level differences were observed: DxN and T clones showed lower performance than the reference DxM group (height: −9.38 cm for DxN, −17.27 cm for T; root biomass: −0.31 g for DxN, −0.65 g for T, Figure 5B). This is consistent with earlier findings that *P. trichocarpa*, *P. nigra* and *P. deltoides* are relatively sensitive to acidic conditions (Naik *et al.* 2009; Smith *et al.* 2011), while hybrids involving *P. maximowiczii* tend to show improved tolerance (Steiner *et al.* 1984).

Heritability estimates indicated a moderate genetic component for height ($H^2 \approx 0.45$, 95% CI: 0.40–0.55) but a low one for root biomass ($H^2 \approx 0.13$, 95% CI: 0.10–0.16, Figure 5A). The lower heritability for root biomass likely reflects the higher plasticity and measurement variability of root traits. Root systems are more plastic than shoots; small differences in root positioning, pot compaction, or O_2 can disproportionately alter root growth, obscuring genetic effects (Meier & Leuschner 2008; Giehl & von Wirén 2014; Chen *et al.* 2022). Moreover, our dry-mass metric omits fine-root traits (number, length, branching, surface area) that drive absorption and are highly Al-sensitive (Poschenrieder *et al.* 2008; McCormack *et al.* 2015; Weemstra *et al.* 2020; Ofoe *et al.* 2023; Fantozzi *et al.* 2024; Rabearison *et al.* 2024). Combined with variance from destructive sampling, this likely reduced signal-to-noise and the heritability of root biomass (Zas & Fernández-López 2005; Giehl & von Wirén 2014), emphasizing the operational advantage of using aboveground growth as the primary screening trait. The strong genetic correlation between height and root biomass ($r = 0.83$) suggests height can be used as a reliable, non-destructive proxy for overall plant vigor in early-stage screening, reducing the cost and labor of destructive sampling. The high genetic correlation between traits also suggests that under Al stress, root–shoot growth is coupled by shared mechanisms. Aluminum disrupts root apex function and nutrient homeostasis (P, K, Ca, Mg); genotypes that sustain uptake and rhizosphere chemistry, including aluminum-activated malate transporter (ALMT) and multidrug and toxic compound extrusion (MATE), mediated exclusion, maintain whole-plant nutrition, photosynthesis, height, and root production (Panda *et al.* 2009; Sun *et al.* 2010; Rahman *et al.* 2018; Liu *et al.* 2022). Al also perturbs auxin/ reactive oxygen species (ROS)/ abscisic acid (ABA) signalling; genotypes that stabilize these can preserve meristem activity and coordinated growth (Kollmeier *et al.* 2000; Sivaguru *et al.* 2000; Liu *et al.* 2016; Wang *et al.* 2016; Yang *et al.* 2017; Li *et al.* 2022), potentially explaining why height under Al stress correlates with root biomass.

To move beyond single-trait ranking, we developed a Composite Tolerance Index (CTI) combining Best Linear Unbiased Predictions (BLUPs) for height with the area under the curve (AUC) from clone-specific dose–response. BLUPs summarize each genotype's genetic merit for a trait after controlling for design effects in a mixed model; they emphasize the heritable signal, shrink noisy estimates toward the mean, and are typically condition-specific (or defined for a modeled average environment). In contrast, AUC integrates performance across the aluminium gradient, capturing both magnitude and stability of growth under increasing stress, i.e., phenotypic plasticity and operational tolerance. Using both distinguishes genetic merit from response breadth and supports more reliable selection under complex, nonlinear stress.

The CTI effectively distinguished tolerant (e.g., T1, MxT1, MxT3, MxT13) from susceptible (e.g., DxN16, DxN11, MxT16, DxN15) clones (Figure 6A). By incorporating both stable genetic performance and plasticity, CTI reduces the risk of selecting clones that perform well only under specific conditions. Similar integrated indices have proven valuable in crop stress breeding (Parent *et al.* 2010; Jarquín *et al.* 2014), but their application in forestry remains rare.

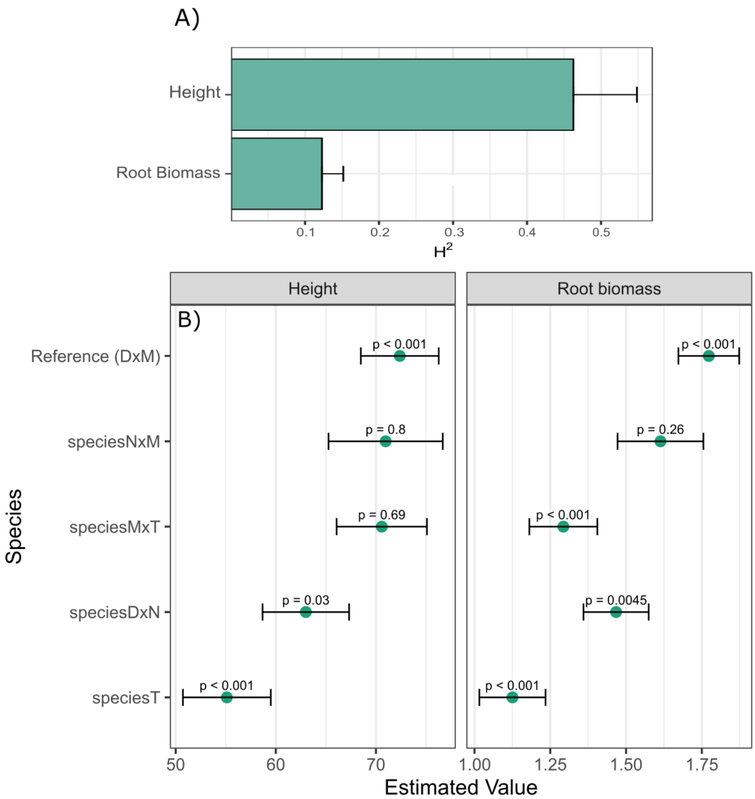

Figure 5. A) Broad-sense heritability (H^2) estimates for final height and root biomass of poplar clones, with 95% confidence intervals derived from the multivariate linear mixed model (MV-LMM). B) Estimated marginal means (EMMs) for height and root biomass across parental species, expressed relative to the reference species (DxM), with 95% confidence intervals and p-values indicating significance.

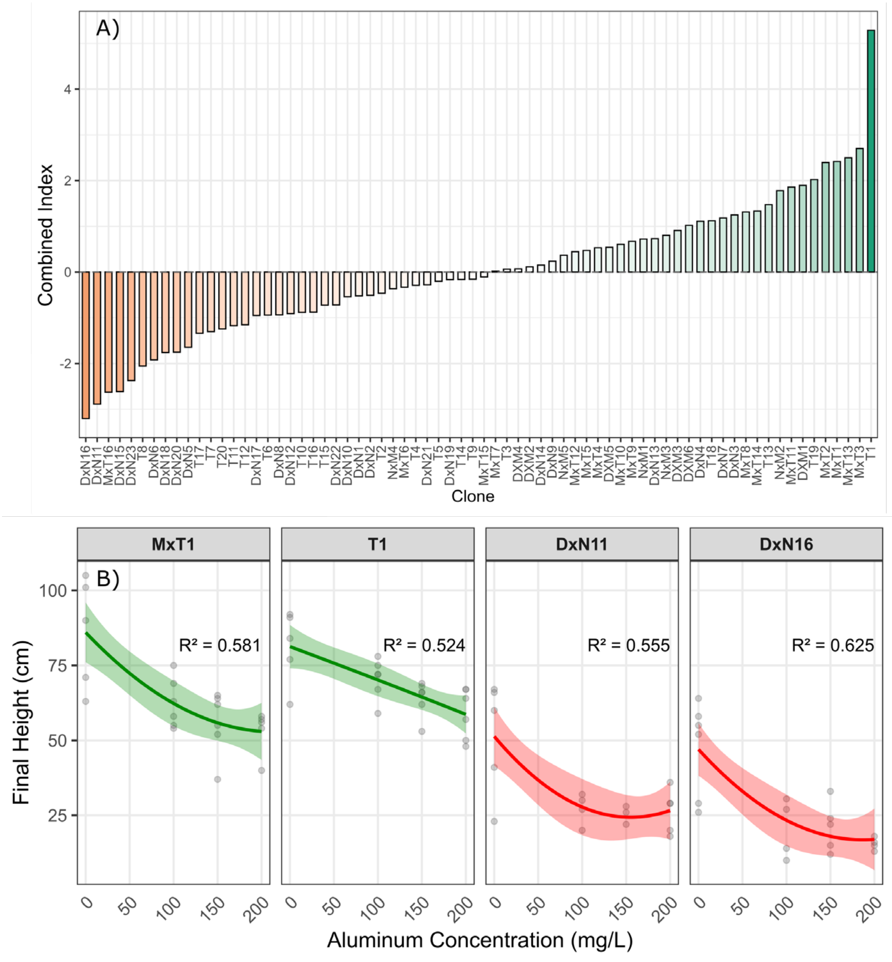

Figure 6. A) Combined aluminium tolerance index for the evaluated poplar clones. The index was calculated by scaling and summing the Best Linear Unbiased Predictions (BLUPs) of final height with the Area Under the Curve (AUC) from clonal dose-response. Positive index values indicate greater aluminium tolerance, whereas negative values indicate lower tolerance. The colour gradient from orange to green represents the continuum from the least to the most tolerant clones. B) Quadratic polynomial relationship between final height and aluminium concentration in selected poplar clones. The figure shows second-degree polynomial regression models describing the relationship between final height (cm) and aluminium concentration (mg L^{-1}) for four clones. Susceptible clones (DxN11 and DxN16) are shown in red, and tolerant clones (MxT1 and T1) in green. Each panel includes the fitted regression curve with a shaded 95% confidence interval and grey dots representing observed values from the screening experiment. The R^2 values in

each panel indicate the proportion of variance in final height explained by the model and reflect model fit for each clone and are useful for evaluating nonlinearity in Al response.

Using the CTI, we selected four clones, two tolerant (T1, MxT1) and two susceptible (DxN11, DxN16), and grew them for 55 days in two contrasting soils: forested arable land (former cropland afforested with Norway spruce 40–70 years ago) and forest soil. Forested arable soils have higher pH and base saturation and lower available Al, whereas forest soils are more acidic, with lower base saturation and higher available Al (Table 1 – Chapter II). Tolerant clones performed consistently across soils (Figure 7A): MxT1 reached ~50 cm and T1 ~45 cm in both soil types by day 55. Susceptible clones grew substantially less in forest soil (DxN11: 30 cm; DxN16: 18 cm) than in forested arable soil (both ~45 cm). Relative growth ratios (forest: forested arable) were close to 1 for tolerant clones but ~0.6 (DxN11) and ~0.4 (DxN16) for susceptible clones.
Morphological data supported these trends. Root and shoot biomass, were unaffected by soil type in tolerant clones but reduced in susceptible clones grown in forest soil (Figure 7B). This validates the greenhouse screening protocol, demonstrating that tolerant clones can sustain performance in acidic, low-fertility soils typical of boreal forestry.

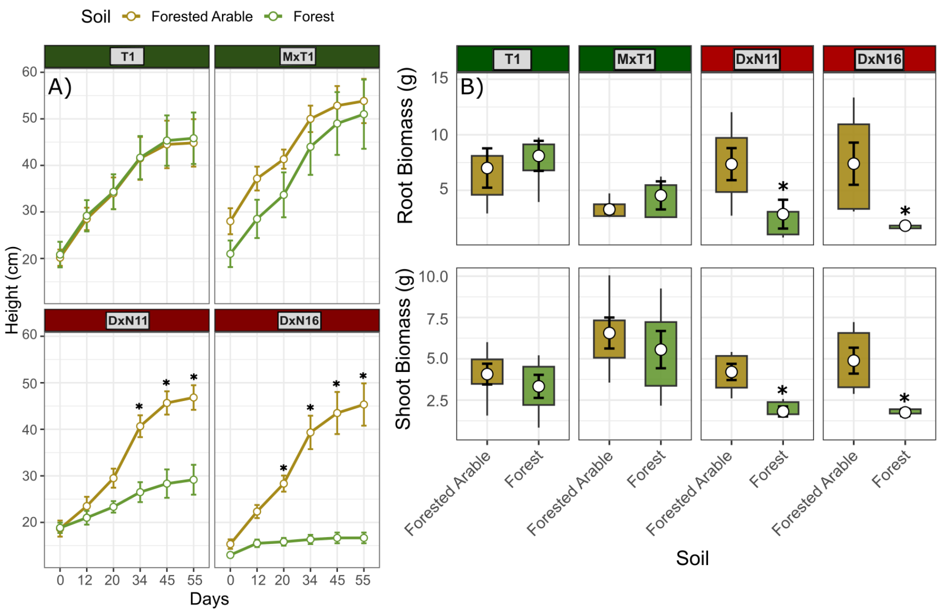

Figure 7. A) Growth trajectories of four poplar clones (T1, MxT1, DxN11, DxN16) over a 55-day period under two soil conditions: forested arable (orange) and forest (green). Height (cm) is shown with error bars representing the standard error of the mean. Asterisks indicate significant differences ($p<0.05$) between soils within the same clone. Green colors represent tolerant clones, while red colors indicate susceptible clones. B) Morphological characteristics of poplar clones under different soil conditions. Boxplots compare the morphological traits of four poplar clones (T1, MxT1, DxN11, DxN16) across two soil types: forested arable and forest. Traits include root biomass and shoot biomass. Each boxplot shows the distribution of values, with the central mark indicating the mean ± standard error, the box edges representing the interquartile range, and whiskers extending to the most extreme non-outlier values. Outliers are shown as individual points. Asterisks (*) indicate statistically significant differences between soil types for a given clone. Colors distinguish tolerant clones (T1 and MxT1, green) from susceptible clones (DxN11 and DxN16, red).

3.2.1 Broader implications for poplar breeding and deployment in acidic soils

These results confirm that aluminium tolerance is not only measurable and heritable but also operationally significant for poplar establishment on acidic forest soils. The identification and deployment of genetically tolerant clones offers several tangible advantages. First, it reduces reliance on costly and logistically challenging soil amelioration measures, such as lime or wood ash, on remote, rugged, or environmentally sensitive sites where machinery access is limited or nutrient additions are constrained by regulation. Second, it expands planting opportunities beyond fertile arable land into underutilised forest soils, many of which are currently excluded from *Populus* cultivation despite their availability. This aligns with diversification targets set out in forest policy and certification frameworks, enabling productive use of sites that would otherwise remain dominated by low-diversity conifer regimes (Felton *et al.* 2016; Bauhus *et al.* 2017). Third, tolerant clones can maintain early growth and survival under conditions that typically cause establishment failures in susceptible material, reducing the risk of stand loss during the critical first years after planting.

The CTI-based selection pipeline developed here can be directly integrated into existing *Populus* breeding programmes. When combined with genomic prediction (Resende Jr *et al.* 2012; Feng *et al.* 2024), it allows for the early identification of superior clones before full phenotyping, significantly shortening breeding cycles. This integration also facilitates multi-trait selection, enabling the simultaneous targeting of aluminium tolerance alongside other resilience traits such as drought tolerance, pest resistance, and browsing tolerance. In a changing climate, this capacity to combine stress-resistance traits in a single breeding framework is likely to become increasingly important.

An important unanswered question concerns the interaction between genetic tolerance and silvicultural interventions such as wood ash application (Chapter III). While tolerant clones may perform well without amendments, it remains unclear whether combining these strategies produces additive benefits, synergistic effects greater than the sum of their parts, or diminishing returns where one intervention masks the effect of the other. These interactions are likely to depend on both site chemistry (pH, base cation levels, Al^{3+} availability) and the genetic background of the clone. Resolving this question will be essential for optimising deployment strategies, maximising cost-effectiveness, and determining where genetic improvement alone is sufficient versus where amendment-based interventions are warranted.

While these results are promising, translating them into operational forestry requires further research. Long-term, multi-site trials are essential to determine whether the tolerance observed in greenhouse and short-term soil experiments persists across full rotations, different climatic zones, and a range of soil chemistries. Such trials should also assess potential trade-offs with wood quality and interactions with other site factors such as moisture regime and vegetation competition. A deeper mechanistic understanding of aluminium tolerance is also needed, including studies on root exudation, rhizosphere chemistry, and transcriptomic responses, to identify the physiological pathways underpinning resilience. This knowledge would support the development of molecular markers for breeding and enable more targeted selection. Finally, the screening–validation framework developed here could be adapted to address other stressors relevant to boreal forestry, such as drought, frost or waterlogging, creating a strategy for breeding and deploying *Populus* clones with multi-trait resilience for a changing climate.

3.3 Soil amendments enhance early growth of poplars on acidic soils (Chapter III)

Wood ash and lime, whether incorporated during soil preparation or applied to the surface, improved early survival and growth of hybrid poplars on both forest (For) and forested arable (ArFor) sites, while biochar gave only minor or delayed benefits. Survival benefits were not immediate, becoming more apparent in the third year, likely reflecting the time needed for amendments to alter soil chemistry and root-zone conditions (Reid and Watmough 2014; Pitman 2006). On For sites, amended plots reached 68–97 % survival compared with lower rates (30-35%) in untreated controls, showing that soil chemical improvement can reduce the establishment risk of poplar on acidic forest soils (Böhlenius & Övergaard 2016; Hjelm & Rytter 2016).

Both wood ash and lime nearly doubled tree height and diameter growth compared to controls, with wood ash producing the largest and most consistent increases (Figure 8). Ash advantage was evident in its ability to sustain high growth (>200 cm by year 3) across a broad range of soil pH, Al, and K levels (Figure 9), due to its broader nutrient profile that includes Ca, Mg, P, K, and several micronutrients (Pitman 2006; Clapham & Zibilske 2008; Johansen *et al.* 2021; Pitman *et al.* 2024). Lime was most effective under low pH and low P but showed diminishing returns at higher pH, P and

Ca. From a soil chemistry perspective, low soil pH increases the solubility of toxic metals, especially Al^{3+} and Mn, damaging root membranes, inhibiting root elongation, and ultimately suppressing shoot growth and survival (Andersson 1988; Ritchie 1989; Foy & Fleming 2015). At the same time, acidity disrupts nutrient balance: Ca^{2+}, Mg^{2+}, and K^{+} are leached from exchange sites, reducing base saturation and cation supply; P becomes fixed to Al/Fe oxides and hydroxides, sharply lowering its plant-available fraction (Schoenholtz *et al.* 2000; Bolan *et al.* 2003; Ashman & Puri 2013; Kish 2024). By increasing pH, lime and wood ash reduce soluble Al^{3+} and Mn^{3+}, alleviating toxicity, especially in Al-sensitive poplars, and likely contributing to the growth increase we recorded (Figure 9D and E). There are though differences in composition and effects between lime and wood ash. Lime primarily supplies Ca and Mg, whereas wood ash also contributes P and K plus micronutrients (Mn, Cu, Mo, Ni). Across both site types, wood ash increased P, K, Ca, Mg, Mn, Zn and raised soil pH, consistent with prior studies (Ohno & Susan Erich 1990; Pitman 2006; Clapham & Zibilske 2008; Johansen *et al.* 2021). We observed greater growth with wood ash, although responses can vary with ash composition (Hakkila 1989; Pitman 2006). Overall, the superior performance under wood ash likely reflects the combined effects of pH amelioration, nutrient supplementation, and reduced metal toxicity, factors critical for early root development and seedling establishment (Grossnickle 2005; Grossnickle & MacDonald 2017).

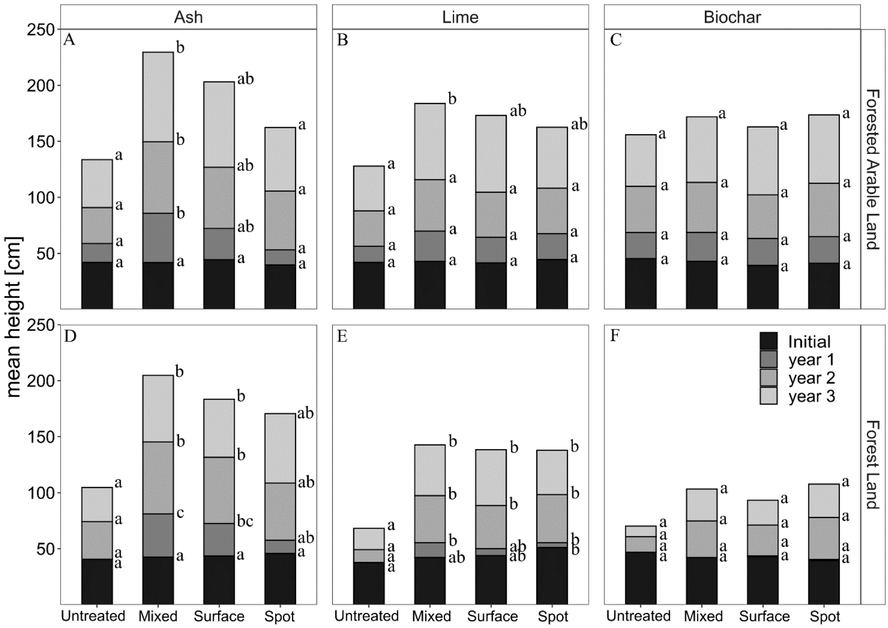

Figure 8. Height growth at forested arable land (ArFor) A to C and forest land (For) D to F. Application of ash are shown in A and D, lime B and E and biochar, C and F. Letters indicate significant differences ($p \leq 0.05$) between the treatments within each year. Note that if a bar is missing, the corresponding yearly growth is too low to be shown.

Biochar's limited short-term effect is consistent with studies that its benefits often require nutrient supplementation or longer time frames to influence pH and nutrient cycling (Thomas & Gale 2015; Dai *et al.* 2017; Joseph *et al.* 2021). The straw-derived biochar used here likely lacked the immediate chemical impact needed for early establishment. However, given its long residence time and potential to improve soil structure and water retention (Kolb *et al.* 2009; Wang *et al.* 2015), biochar may still have value as a slow-acting amendment in combination with faster-acting materials such as ash, a possibility that warrants longer-term trials (Palviainen *et al.* 2020; Grau-Andrés *et al.* 2021).

Application method, mixed during soil preparation or applied to the surface, had little influence on growth (Figure 8), indicating operational flexibility. This allows managers to select methods based on site accessibility, equipment availability and cost, with surface application also offering potential for mid-rotation applications or drone-based spreading (Guan *et al.* 2019; Rejeb *et al.* 2022).

Overall, wood ash, and lime under certain site conditions, could help close the productivity gap between poplar plantations on arable versus forested arable land. While regulatory limits on non-native species persist on forest land, forested arable land offers opportunities for targeted deployment, particularly under policies encouraging broadleaf planting (Sveriges regering 2021).

Beyond productivity gains, amendment choice also carries sustainability implications. Wood ash offers advantages over lime as it is a by-product of bioenergy production, enabling nutrient recycling and reducing waste streams (Pitman 2006). Its use supports circular bioeconomy objectives and aligns with Swedish policy promoting the return of forest-derived nutrients to the soil. However, ash quality can vary between sources and may contain trace metals, requiring careful quality control and compliance with application guidelines (Karltun *et al.* 2008; Lindvall *et al.* 2015). Lime, in contrast, is mined and processed, resulting in a higher carbon footprint from extraction, grinding, and transport, estimated at up to 0.75 Mg CO_2 per Mg of lime produced (European Commission 2001; European Commission 2010). While more chemically consistent than ash, lime does not recycle nutrients removed from forest biomass. In operational forestry, wood ash therefore represents a more sustainable amendment where supply chains and quality standards are well developed (da Costa *et al.* 2020), while lime remains a useful option where ash is unavailable or unsuitable for specific soil conditions. Selecting between these materials thus depends not only on site chemistry and operational constraints but also on broader sustainability and policy goals for forestry diversification.

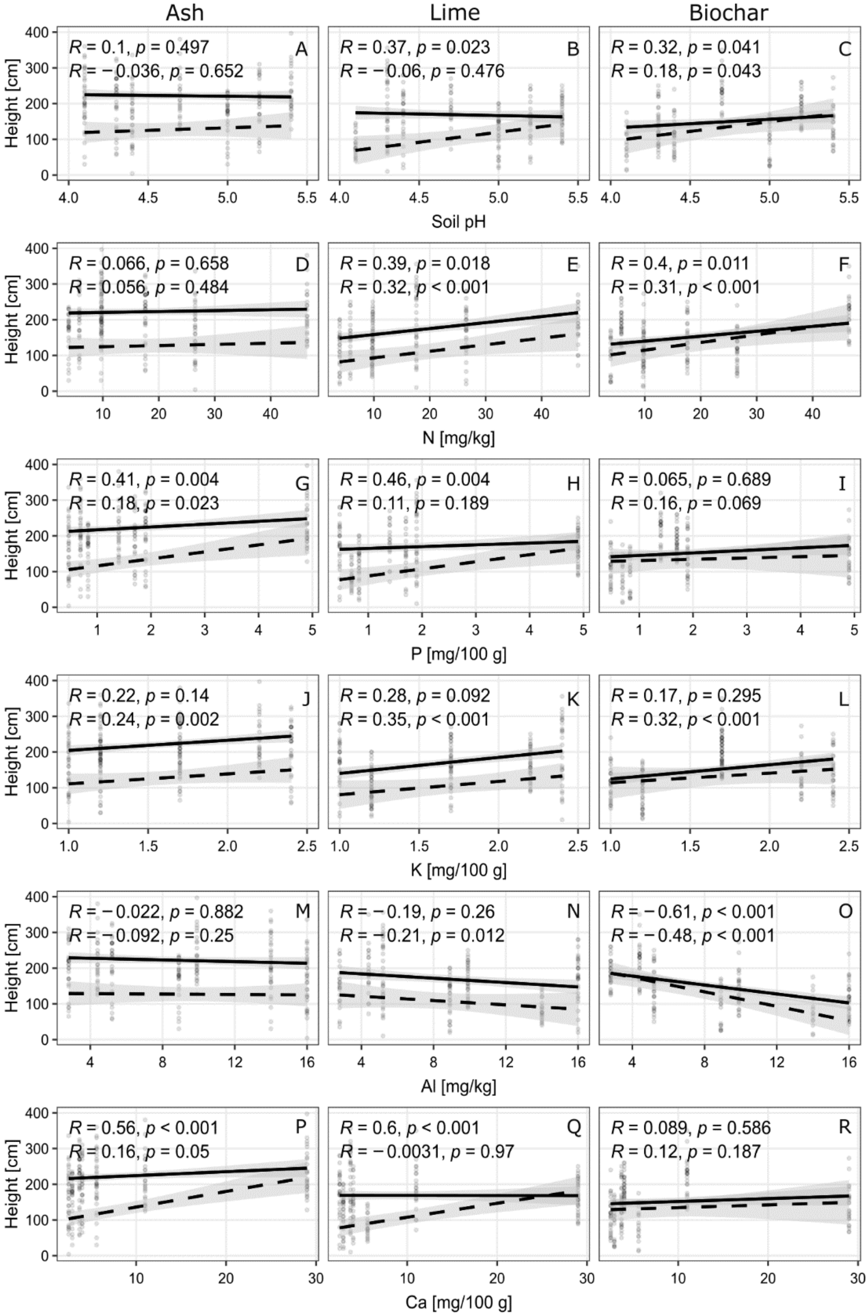
Ash
Lime
Biochar
Height [cm]
R = 0.1, p = 0.497
R = −0.036, p = 0.652
A
R = 0.37, p = 0.023
R = −0.06, p = 0.476
B
R = 0.32, p = 0.041
R = 0.18, p = 0.043
C
Soil pH
R = 0.066, p = 0.658
R = 0.056, p = 0.484
D
R = 0.39, p = 0.018
R = 0.32, p < 0.001
E
R = 0.4, p = 0.011
R = 0.31, p < 0.001
F
N [mg/kg]
R = 0.41, p = 0.004
R = 0.18, p = 0.023
G
R = 0.46, p = 0.004
R = 0.11, p = 0.189
H
R = 0.065, p = 0.689
R = 0.16, p = 0.069
I
P [mg/100 g]
R = 0.22, p = 0.14
R = 0.24, p = 0.002
J
R = 0.28, p = 0.092
R = 0.35, p < 0.001
K
R = 0.17, p = 0.295
R = 0.32, p < 0.001
L
K [mg/100 g]
R = −0.022, p = 0.882
R = −0.092, p = 0.25
M
R = −0.19, p = 0.26
R = −0.21, p = 0.012
N
R = −0.61, p < 0.001
R = −0.48, p < 0.001
O
Al [mg/kg]
R = 0.56, p < 0.001
R = 0.16, p = 0.05
P
R = 0.6, p < 0.001
R = −0.0031, p = 0.97
Q
R = 0.089, p = 0.586
R = 0.12, p = 0.187
R
Ca [mg/100 g]

Figure 9. Linear regression of tree height after three growing seasons vs. soil proprieties. Panels A-C show soil pH with plants treated with A) wood ash, B) lime, C) biochar. Panels D-F show total nitrogen (N) with plants treated with, D) wood ash, E) lime, F) biochar. Panels G-I show phosphorus (P) with plants treated with G) wood ash, H) lime, I) biochar. Panels J-L show potassium (K) with plants treated with J) wood ash, K) lime, L) biochar. Panels M-O show aluminium (Al) with plants treated with M) wood ash, N) lime, O) biochar. Panels P-R show calcium (Ca) with plants treated with P) wood ash, Q) lime, R) biochar. The solid line represents plants treated with the respective soil amendment by the Mixed method, while the dashed line represents untreated plants. The R-value displayed at the top corresponds to the treated poplars (solid line), whereas the lower R-value represents the untreated poplars (dashed line). Confidence bands represent a 95% confidence interval.

3.4 Wood ash as a silvicultural amendment: evidence from the literature (Chapter IV)

This review of 41 studies spanning more than three decades provides a comprehensive synthesis of wood ash effects on the growth of temperate and boreal broadleaf tree species. While the diversity of study designs, ash sources, doses, and site types produced variable outcomes, several consistent patterns emerge, with direct implications for the use of ash as a silvicultural amendment in Sweden.

Across genera, soil type was the single most important factor shaping tree growth responses. Organic soils, typically acidic and nutrient-poor, showed consistently stronger positive responses to ash application than mineral soils, in agreement with earlier syntheses (Augusto *et al.* 2008). This pattern reflects the combined effect of pH correction, replenishment of base cations such as calcium (Ca), potassium (K), and magnesium (Mg), and improved phosphorus (P) availability, which are particularly limiting in drained peatlands (Schwärzel *et al.* 2002; Pitman 2006). On mineral soils, responses were more variable and often neutral at low to moderate doses, with occasional growth suppression at very high rates (>20 Mg ha^{-1}), likely due to nutrient imbalances, osmotic stress, or metal toxicity (Gupta *et al.* 2002; Aronsson & Ekelund 2004).

A clear dose–response trend was evident across species. Low to moderate ash applications (0.5–9.9 Mg ha^{-1}) were most often associated with neutral to moderately positive effects on height, diameter, and biomass. Benefits rarely increased beyond this range, and in some cases plateaued or reversed at high doses, consistent with risks of nutrient imbalance or metal toxicity

(Gupta *et al.* 2002; Aronsson & Ekelund 2004). Willows on organic soils were a notable exception, maintaining positive biomass responses even above 20 Mg ha^{-1} (Hytonen 1998). These patterns support current Swedish Forest Agency recommendations for moderate dosing, particularly on peatland forests and nutrient-rich mineral sites (Emilsson 2006).

While soil and dose effects were consistent, species and even genotypes within species displayed distinct responses. Silver birch (*B.pendula*) on organic soils responds reliably and often strongly to ash at low–moderate rates (≤ 10 Mg ha^{-1}) across ages and settings, with frequent gains in height, diameter, biomass, and MAI (Huotari *et al.* 2008; Hytönen 2016; Makovskis *et al.* 2023). Very high doses add little or can be neutral (Lumme 1988; Hytönen 2016). On mineral soils, responses are mostly neutral in both young and older stands (Brandtberg *et al.* 2021; Makovskis *et al.* 2023; Pitman *et al.* 2024). Downy birch (*B. pubescens*) broadly mirrors these patterns, while paper birch (*B. papyrifera*) on mineral soil was largely unresponsive (Williams & Thomas 2024). In summary, ash is a dependable tool for *Betula* on peat/organic sites, but evidence is weaker for mineral soils.

For poplars, evidence is thinner and highly context dependent. On mineral soils, low–moderate doses (≈0.5–9.9 Mg ha^{-1}) tend to yield neutral to modest positive effects in young stands, with magnitude contingent on soil chemistry (Lazdiņa *et al.* 2014; Szabó *et al.* 2016; Muraro *et al.* 2025). Greenhouse work shows that very high doses can depress growth (Etiegni *et al.* 2008), while moderate additions sometimes help biomass or diameter (Cavaleri *et al.* 2004; Aggarwal & Goyal 2009). Critically, no field tests exist on organic soils and few data are available for older stands, key gaps for deployment on acidic or peaty sites where poplar establishment is often constrained.

Willows (*Salix* spp) show the clearest benefits on organic soils: low–moderate doses improve height and biomass in young stands and increase biomass or MAI in older stands; even >20 Mg ha^{-1} can remain beneficial in peat (Hytonen 1998; Hytönen & Kaunisto 1999; Huotari *et al.* 2008; Huotari *et al.* 2009). On mineral soils, responses are mixed and clone- or dose-dependent, with more consistent gains around 10–19.9 Mg ha^{-1} in young stands (Park *et al.* 2004; Rodzkin & Krstic 2022; Williams & Thomas 2024). These results highlight willow as a strong candidate for ash recycling on peat, though application on mineral soils should be selective.

Alders are highly species- and context-specific. *Alnus glutinosa* on organic soils often benefits at both low and higher doses under field conditions (Neimane *et al.* 2019; Neimane *et al.* 2021), whereas greenhouse responses are less consistent (Pärn *et al.* 2009). On mineral soils, *A. incana* and hybrids are frequently neutral or negative (Makovskis *et al.* 2023), with only limited gains where nitrogen was co-applied(Hytönen & Saarsalmi 2015). One study reported hybrid-alder biomass gains despite ash negligible nitrogen content (Bertins *et al.* 2023), hinting at indirect pH or cation effects. In practice, ash appears suitable for *A. glutinosa* on organic soils, but evidence elsewhere is weak or adverse.

Other broadleaves show limited evidence. Hybrid aspen on mineral soils displays clone-specific, mainly small or neutral effects at 6–9.9 Mg ha^{-1} (Bardule *et al.* 2013; Makovskis *et al.* 2023). *Populus tremuloides* is generally neutral across 6–19.1 Mg ha^{-1} (Feldkirchner *et al.* 2003; Williams & Thomas 2024). *Acer saccharum* and *A. rubrum* are largely neutral in both field and greenhouse studies (Unger & Fernandez 1990; Feldkirchner *et al.* 2003; Noyce *et al.* 2017; Arseneau *et al.* 2021). *Quercus robur* shows a small height gain at 0.5–5.9 Mg ha^{-1} in older stands (Pitman *et al.* 2024). Overall, studies for these taxa are sparse, limiting result interpretation and clear recommendations.

The chemical composition of ash varied widely among studies (P: 0.7–36 g kg^{-1}, K: 2.1–119 g kg^{-1}, Ca: 43.9–350 g kg^{-1}, pH: 6.1–13.3), reflecting differences in biomass origin, combustion conditions, and fraction (fly vs. bottom ash). Such variability reinforces the need for pre-application analysis and site-specific management prescriptions (Lindvall *et al.* 2015).

The beneficial effects of ash are likely mediated through multiple mechanisms. These include pH correction in acidic soils, reducing the solubility and toxicity of Al^{3+} and Mn^{3+} ions (Marschner 1991; Pitman 2006); nutrient replenishment, especially of potassium (K), phosphorus (P), calcium (Ca), and magnesium (Mg), which offsets deficits exacerbated by whole-tree harvesting (Clapham & Zibilske 2008); improved soil structure and cation exchange capacity, particularly in peat substrates (Schwärzel *et al.* 2002; Karltun *et al.* 2008); and longer-term fertility effects through gradual nutrient release and base saturation increase (Lundström *et al.* 2003).

Despite the breadth of literature reviewed, the evidence base remains uneven across taxa, site types, and stand ages. The near-absence of long-term (>15 years) studies limits our understanding of growth effects into mid-rotation

(Aronsson & Ekelund 2004). Research on ash application in organic soils for *Populus* spp. is lacking, despite the species sensitivity to pH and nutrient status (Andersson 1988; Silva & Beeson 2011). Clone-level trials for genetically diverse species such as willow and hybrid aspen are rare, and broadleaf species beyond birch, willow, and alder remain underrepresented in both field and greenhouse contexts.

From a management perspective, this synthesis supports targeted use of wood ash on organic soils for *Betula* spp., *Salix* spp., and *Alnus glutinosa* to improve early establishment and potentially shorten rotation lengths (Huotari *et al.* 2008; Hytönen 2016; Bertins *et al.* 2023). For *Populus* spp., particularly hybrids poplars used in biomass plantations, ash application may be beneficial on certain mineral soils, but prescriptions should be informed by site chemistry (Muraro *et al.* 2025). Integrating ash recycling into forest management aligns with circular bioeconomy principles and can offset nutrient exports from intensive harvesting (Karltun *et al.* 2008; da Costa *et al.* 2020), though its role should be balanced with biodiversity, soil carbon, and certification considerations.

3.5 General limitations

While the studies in this thesis provide complementary insights into the establishment of *Populus* species on acidic forest soils, several limitations should be acknowledged. First, the field trials span only the early establishment phase (three years), leaving longer-term growth, rotation-scale productivity, and resilience under climate extremes uncertain. Given the relatively short monitoring periods, conclusions on the sustainability of soil amendments or genetic tolerance over time remain preliminary.

Second, both field and greenhouse experiments represent simplified contexts. The greenhouse screening of aluminium tolerance allowed rigorous control of environmental variables but may not fully capture the complexity of soil–plant–microbe interactions in operational settings. Similarly, field trials were conducted under fenced conditions, which likely reduced the influence of browsing compared with unfenced operational plantings.

Third, while clonal variation in aluminium tolerance was demonstrated, the genetic base was limited to available breeding material, and broader geographic testing across contrasting site conditions was beyond the scope of this work. The absence of large-scale or long-term data constrains the ability to assess genotype × environment interactions and long-term adaptation.

Fourth, soil amendment experiments focused on wood ash, lime, and biochar at operationally relevant doses and methods, but did not explore interactions with fertilization, mixed amendments, or different ash chemistries in depth.

Finally, the systematic review synthesized evidence from 41 studies but was limited by heterogeneity in reporting, lack of standardized growth metrics, and underrepresentation of certain taxa (e.g., *Populus* spp. on organic soils). The absence of meta-analysis means that effect sizes could not be quantified across contexts.

Together, these limitations highlight the need for longer-term monitoring, broader clonal testing, and integrated trials that combine genetic selection with silvicultural treatments under realistic operational conditions.

4. Overcoming establishment challenges for poplars in Swedish forestry

4.1 A dual-track strategy for poplar establishment

Taken together, the findings from this thesis point to a dual-track strategy for overcoming establishment constraints of poplar on non-arable sites in Sweden. This approach recognizes that no single intervention will address the diversity of site conditions, operational constraints, and future climate challenges facing Swedish forestry.

The comparative experiment across species and site types (Chapter I) set the stage by showing that establishment success is not determined by site fertility alone. Birch, and hybrid aspen established more successfully on forest soils than on forested arable soils, while conifers combined modest growth with high mortality on fertile sites where competing vegetation was abundant. Poplars (without ash application), in contrast, struggled across both site types, with lower survival and growth than competing species. These findings highlighted that for poplar, general site fertility is not enough, specific barriers such as soil acidity, nutrient imbalances, and competitive stress must be addressed directly. This recognition provided the rationale for developing targeted strategies in the subsequent chapters.

1. Genetic pathway – Deploying aluminium-tolerant clones on the most acidic, low-fertility sites offers a way to overcome chemical barriers without ongoing external inputs. The clone screening and validation (Chapter II) demonstrated that tolerance is heritable, predictable from early testing, and effective in maintaining growth under forest soil conditions. This pathway is particularly suited to remote or environmentally sensitive sites where amendment application is impractical or costly, such as in upland forest stands, protected catchments, or areas with limited road access. By leveraging inherent genetic resilience, this approach reduces both establishment risk and the long-term reliance.

2. Silvicultural pathway – On sites within operational reach, applying wood ash can create conditions that allow a broader pool of poplar genotypes to thrive. The field amendment trials (Chapter III) and the systematic review (Chapter IV) show that wood ash can simultaneously correct soil acidity and supply multiple macro- and micronutrients. This enables the deployment of high-yielding but potentially less tolerant clones, closing the 20–45%

productivity gap often observed between arable and non-arable poplar plantations. Given Sweden's policy interest in recycling industrial by-products, this pathway also aligns with circular bioeconomy objectives and offers a means of valorising residues from bioenergy production.

Rather than competing alternatives, these pathways are mutually reinforcing. The genetic pathway extends the geographic and soil requirement range where poplar can be grown without intervention, while the silvicultural pathway maximizes yield potential where interventions are feasible. In combination, they broaden the range of sites suitable for poplar plantations, support diversification targets within FSC (≤ 5%) and PEFC (≤ 20%) non-native species limits, and offer a flexible toolkit that can be adapted to local site conditions and management objectives.

However, the combined effect of genetic and silvicultural interventions effect on poplar establishment remains unknown. In principle, their impacts could be additive, resulting in even greater establishment success when applied together, or they could interact in non-linear ways, with one factor overriding the other. For example, strong genetic tolerance might reduce the relative benefit of amendments, or amendments might mask genetic differences by alleviating the underlying stress. Determining the nature and magnitude of these interactions will be essential for designing cost-effective deployment strategies that maximize both biological and economic returns.

4.2 Outlook and research needs

Long-term, multi-site field validation – The trials in this thesis covered the first 3 years after planting, but poplar rotations in Sweden often extend to 20 years. Multi-site, long-term field trials are needed to determine whether the early growth advantages observed here translate into sustained productivity and profitability. Such trials should encompass a variety of climatic regions and soil types to capture variability in drought frequency, pest pressures, and frost exposure.

Breeding for multi-trait resilience – Climate projections for southern and central Sweden indicate warmer, drier summers, which could interact with soil acidity and nutrient limitations in complex ways (Kronnäs et al 2023). Future breeding programs should integrate aluminium tolerance with traits such as drought resilience, pest resistance, and browsing tolerance. The strong genetic correlation between above- and belowground growth found in this thesis (Chapter II) suggests that efficient early selection is possible. Genomic selection (Resende et al., 2012), combined with clonal propagation and targeted hybridization (Grattapaglia et al., 2018; Sunny et al., 2021), can shorten breeding cycles from decades to years, enabling faster delivery of adapted planting material.

Refining amendment application – The experimental and review findings (Chapter III and IV) support moderate wood ash doses as a general recommendation for acidic soils, but optimal prescriptions for poplar require further refinement. Research should explore ash composition variability, interaction with other amendments such as biochar, and the timing and frequency of applications. There is also scope to investigate operational innovations such as drone-based or precision band application, which could reduce costs and environmental disturbance while targeting areas of greatest need.

Bridging knowledge gaps in the literature – The systematic review (Chapter IV) highlighted significant gaps for *Populus* on organic soils, in high-competition environments, and in clone-specific responses to amendments. Addressing these gaps will require integrating genotype × environment trials with soil chemistry monitoring and vegetation management studies. Expanding the evidence base to include a wider range of *Populus* taxa is essential for building robust silvicultural recommendations.

Integrating pathways into operational forestry – The ultimate test of the dual-track strategy is adoption in real-world management. Demonstration sites and partnerships with forest companies, municipalities, and private landowners could showcase the feasibility and benefits of deploying tolerant clones and/or using targeted amendments. These initiatives would also provide a platform for monitoring ecosystem service co-benefits such as carbon sequestration, biodiversity enhancement, and nutrient recycling.

Beyond the biological and silvicultural dimensions, future research should address the socio-economic and policy contexts that will ultimately determine the feasibility of poplar deployment. Even if tolerant clones and targeted ash amendments prove biologically effective, their adoption depends on cost–benefit trade-offs, logistical practicality, and landowner perceptions. Comparative analyses of establishment costs and long-term returns across species, treatments, and site types could clarify where poplar represents a competitive option. Equally important is understanding landowner motivations and risk tolerance, since perceptions of non-native species, amendment use, or market uncertainty can strongly shape uptake.

Certification and regulatory frameworks also require attention. Poplar deployment should fit within FSC and PEFC restrictions on non-native species, and ash application must comply with environmental standards governing nutrient balances and heavy metal concentrations. Research is needed to clarify how tolerant clones and ash recycling interact with biodiversity objectives, soil carbon dynamics, and watershed protection, all of which influence the social motive for expansion. Such work could help ensure that the dual-track strategy aligns with broader policy goals on climate mitigation and sustainable bioeconomy.

Future studies should also consider ecosystem service synergies and trade-offs. Beyond wood production, poplar plantations may contribute to carbon sequestration, water regulation, nutrient cycling, and landscape diversification. At the same time, trade-offs with biodiversity conservation, soil organic matter retention, or groundwater chemistry need systematic evaluation. Framing poplar deployment within a multifunctional forestry perspective could strengthen its legitimacy as part of Sweden diversification strategy.

Taken together, this broader agenda highlights that successful deployment of poplar in Sweden depends not only on biological breakthroughs but also on integrating silvicultural innovations with socio-economic feasibility, certification compliance, and ecosystem service goals. By addressing these multiple dimensions, poplar can transition from a niche species on arable land to a cornerstone of climate-smart diversification in Swedish forestry.

Ultimately, the establishment of poplar on acidic forest soils should not be viewed in isolation but as part of Sweden's broader diversification agenda. With spruce-dominated forests increasingly vulnerable to pests, storms, and climate extremes, introducing fast-growing broadleaves like poplar and hybrid aspen can spread risks and complement birch in mixed-forest strategies. By showing that genetic tolerance and targeted silviculture can open new site types for poplar, this thesis illustrates how diversification targets can be met (within certification limits) while simultaneously contributing to climate adaptation, circular bioeconomy goals, and a more multifunctional forest landscape. In this sense, the dual-track strategy developed here is not only a tool for improving poplar establishment, but also a pathway to strengthening the resilience and diversity of Swedish forestry.

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Popular science summary

Forestry in Sweden has long been dominated by two conifers: Norway spruce and Scots pine. These species have formed the backbone of the forest industry for centuries, supplying timber, pulp, and paper. But recent decades have shown the vulnerabilities of such a narrow base. Climate change is bringing more frequent storms, droughts, and pest outbreaks, particularly the devastating bark beetle infestations that have affected spruce forests across central and southern Sweden. At the same time, public debate about biodiversity and certification standards is putting pressure on the sector to diversify species composition.

One group of trees that has attracted attention as an alternative is *Populus*: poplars, aspens, and their hybrids. These are among the fastest-growing trees in the temperate and boreal zones. In other parts of the world, such as China, North America, and continental Europe, they are widely planted for timber, paper, and bioenergy production. In Sweden, hybrid aspen and certain poplar hybrids have been tested with good results on fertile farmland, where yields can be very high. But farmland is scarce and competing with food production, so the real challenge is whether these species can also be grown successfully on forest soils, which are more acidic and nutrient-poor.

The central theme of this thesis is therefore how to overcome the barriers that prevent poplars from establishing on Swedish forest soils. To investigate this, field experiments, genetic screening, soil chemistry studies, and a systematic review of international research were combined.

In large-scale field experiments, poplars were planted alongside birch, aspen, hybrid aspen, spruce, and pine. Two contrasting site types were studied: long-term forest land, and forested arable land (former agricultural land that had been planted with spruce for one rotation). The results were striking. On forest land, hybrid aspen and birch established best, while spruce and pine also survived relatively well. Poplars, however, struggled on these acidic soils unless they received wood ash treatment. On forested arable land, untreated poplar performed poorly, but when treated with wood ash it not only survived but often outperformed spruce and pine. This showed that poplars have strong potential, but only if site limitations are addressed.

One of the main reasons poplars fail on acidic soils is aluminium toxicity. When soil pH drops below 5, aluminium becomes soluble and damages roots, preventing normal water and nutrient uptake. While aspens are naturally more tolerant, many poplar hybrids are highly sensitive. To test whether genetic differences could be used to overcome this problem, 70 different clones (genetically distinct individuals) were screened under greenhouse conditions. Wide variation was observed: some clones maintained good growth even under high aluminium levels, while others suffered major reductions in height and root biomass. Statistical models revealed that height is a reliable indicator of tolerance and is moderately heritable, meaning that this trait can be selected for in breeding. By combining genetic predictions with actual growth responses, a Composite Tolerance Index (CTI) was developed to identify the most robust clones.

Since controlled greenhouse experiments provide only part of the answer, tolerant and sensitive clones were also planted in acidic forest soil and forested arable soil. The outcome confirmed the greenhouse findings: tolerant clones grew equally well in both soil types, while sensitive clones performed much worse in forest soil. This validation step was crucial, as it showed that clone choice can determine whether establishment succeeds or fails.

In parallel, soil amendments were tested to improve establishment. Wood ash, a by-product from bioenergy plants, is already used in some parts of forestry to return nutrients removed during harvest. Lime and biochar were also included for comparison. Across multiple field sites, wood ash consistently gave the best results, especially when it was mixed into the soil at planting. It raised pH, supplied calcium, magnesium, and potassium, and improved survival and growth of poplar. Lime also had positive effects but was less consistent, while biochar showed limited benefits under the conditions tested. Importantly, however, the effects of amendments varied depending on soil type and application method. This means that while wood ash is promising, it cannot be seen as a "one size fits all" solution.

To place these findings in a broader context, a systematic review of 41 studies from Europe, North America, and Asia was carried out. The results showed that wood ash usually improves the growth of broadleaved trees on acidic or nutrient-poor soils. However, responses depend on tree species, soil type, and application rate, and excessive ash can even be harmful. The review highlighted both the opportunities and the limits of using ash as a silvicultural tool.

Taken together, the results of this thesis point to a dual strategy for establishing poplars in Sweden:

- Genetic selection – using clones that are tolerant to aluminium stress and better adapted to acidic soils.
- Targeted soil amendments – applying wood ash or other treatments when soil conditions are too limiting.

By combining these approaches, poplars and other fast-growing broadleaves could be grown not only on farmland but also on more widely available forest soils. This would make Swedish forestry more diverse and resilient, help reduce risks associated with climate change and pests, and provide a sustainable supply of renewable raw material.

The thesis also highlights a shift in thinking. Instead of asking “Can poplars grow on forest soils?” the more relevant question is “Under what conditions can they succeed?” The answer lies in smart combinations of the right genetic material and the right site management. In practice, this could mean planting tolerant clones on more remote or less fertile forest soils where soil amendments are impractical, while using ash treatment to boost establishment on sites where it is feasible.
Such approaches align with the goals of climate-smart forestry and certification standards, which encourage diversification and sustainable management. They also point to future opportunities in breeding programs, where tolerance to aluminium could be combined with other traits such as drought resistance or pest resilience. In a changing climate, these multiple layers of adaptation will be essential.

Populärvetenskaplig sammanfattning

Svenskt skogsbruk har länge dominerats av två barrträd: gran och tall. Dessa arter har i århundraden utgjort ryggraden i skogsindustrin och försett samhället med virke, massa och papper. Men de senaste decennierna har visat på sårbarheten i en så smal bas. Klimatförändringar medför fler stormar, torkperioder och skadeangrepp, särskilt barkborreangreppen som har slagit hårt mot gran i stora delar av södra och mellersta Sverige. Samtidigt ställer den offentliga debatten om biologisk mångfald och certifieringskrav ökade krav på en mer diversifierad trädslagsblandning.

En grupp träd som fått ökad uppmärksamhet som alternativ är popplar och hybridaspar. Dessa hör till de snabbast växande träden i den tempererade och boreala zonen. I länder som Kina, Nordamerika och Centraleuropa används de i stor skala för virke, papper och bioenergi. I Sverige har hybridasp och vissa poppelhybrider testats med goda resultat på bördig jordbruksmark, där tillväxten kan vara mycket hög. Men jordbruksmark är en begränsad resurs och konkurrerar med livsmedelsproduktion. Den verkliga utmaningen är därför om popplar också kan etableras på skogsmarker, som ofta är sura och näringsfattiga.

Denna avhandling har som tema att förstå och övervinna de hinder som begränsar popplarnas etablering på svenska skogsmarker. För att undersöka detta har fältexperiment, genetiska studier, markkemiska analyser och en systematisk litteraturöversikt kombinerats.

I storskaliga fältexperiment planterades popplar tillsammans med björk, asp, hybridasp, gran och tall. Två marktyper jämfördes: långvarig skogsmark och skogsbevuxen åkermark (tidigare jordbruksmark planterad med gran i en omloppstid). Resultaten var tydliga. På skogsmark etablerade sig hybridasp och björk bäst, medan gran och tall också överlevde relativt väl. Popplar däremot hade svårt att klara sig på dessa sura marker – om de inte fick behandling med aska. På skogsbevuxen åkermark gick det dåligt för obehandlad poppel, men med askbehandling överträffade den ofta både gran och tall. Detta visade att popplar har stor potential, men bara om markbegränsningarna hanteras.

En huvudorsak till misslyckad etablering är aluminiumtoxicitet. När pH sjunker under 5 blir aluminium lösligt och skadar rötterna, vilket hindrar upptag av vatten och näring. Asp är naturligt mer tålig, men många poppelhybrider är känsliga. För att undersöka om genetiska skillnader kan utnyttjas testades 70 olika kloner i växthus. Variationerna var stora: vissa kloner växte bra även vid höga aluminiumhalter, medan andra drabbades av kraftig tillväxtnedsättning. Statistiska analyser visade att höjd är en pålitlig indikator på tolerans och måttligt ärftlig – en egenskap som kan utnyttjas i förädling. Genom att kombinera genetiska prognoser med faktiska tillväxtdata utvecklades ett samlat toleransindex (CTI) för att identifiera de mest robusta klonerna.

Eftersom växthusförsök inte ger hela bilden planterades både tåliga och känsliga kloner även i sur skogsjord och i skogsbevuxen åkermark. Resultaten bekräftade växthusstudien: tåliga kloner växte lika bra i båda jordtyperna, medan känsliga kloner presterade sämre i skogsjord. Detta visade att klonvalet kan avgöra om etableringen lyckas eller misslyckas.

Parallellt testades markförbättringar för att underlätta etablering. Träaska – en restprodukt från bioenergianläggningar – används redan i viss utsträckning för att återföra näringsämnen efter skörd. Även kalk och biokol ingick i försöken. På flera fältförsök gav aska genomgående bäst resultat, särskilt när den blandades in i jorden vid plantering. Den höjde pH, tillförde kalcium, magnesium och kalium och förbättrade popplarnas överlevnad och tillväxt. Kalk hade också positiva effekter men var mindre tillförlitlig, medan biokol visade begränsade resultat under de aktuella förhållandena. Effekterna varierade dock med jordtyp och spridningsmetod, vilket visar att aska inte är en universallösning.

För att sätta resultaten i ett större sammanhang genomfördes en systematisk översikt av 41 internationella studier. Den visade att träaska oftast förbättrar bredbladiga trädarters tillväxt på sura eller näringsfattiga marker. Effekten beror dock på trädslag, jordtyp och dos, och för höga givor kan vara skadliga.

Sammantaget pekar resultaten på en dubbel strategi för att etablera popplar i Sverige:

Genetiskt urval – användning av kloner som är toleranta mot aluminiumstress och bättre anpassade till sura jordar.

Riktade markförbättringar – tillförsel av träaska eller andra behandlingar där markförhållandena är för begränsande.

Genom att kombinera dessa angreppssätt kan popplar och andra snabbväxande lövträd etableras inte bara på jordbruksmark utan också på mer allmänt tillgängliga skogsmarker. Detta skulle göra svenskt skogsbruk mer diversifierat och motståndskraftigt, minska riskerna med klimatförändringar och skadegörare samt bidra med en hållbar råvaruförsörjning.

Avhandlingen markerar också ett skifte i perspektiv: istället för att fråga ”Kan popplar växa på skogsmark?” är den mer relevanta frågan ”Under vilka förhållanden kan de lyckas?” Svaret ligger i smarta kombinationer av rätt genetiskt material och rätt markbehandling. I praktiken kan det innebära att plantera toleranta kloner på avlägsna eller magra marker där markförbättringar inte är möjliga, medan askbehandling kan användas där det är praktiskt genomförbart.

Dessa strategier ligger i linje med målen för klimatsmart skogsbruk och certifieringsstandarder, som betonar diversifiering och hållbart brukande. De pekar också framåt mot nya möjligheter i förädlingsprogram, där aluminiumtolerans kan kombineras med egenskaper som tork- eller skadeinsektresistens. I ett förändrat klimat blir sådana lager av anpassning avgörande.

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Well… four years gone already. Did I have fun? Hell yeah. But this ride has been way more than just fun; stress, excitement, frustration, accomplishment, boredom… and about a hundred other emotions in between.

Just like a good meal, every journey is better when shared. I can't name everyone who's helped me get here, but I'll give it a shot.

First, a word of thanks to my main supervisor, Henrik B. The first rodeo for both of us. We had to figure each other out along the way (sometimes the hard way) but hey, we got there in the end. Thanks for sticking it out and for the support throughout this ride. An equally sized thanks goes to my co-supervisors, Mateusz and Kathryn, and to Anneli as well, not officially on the team, but definitely part of it. Thanks also to the Super Meetings crew (Michalina, Iida, Tanya, and Sara) for all the stimulating discussions! Michalina and Iida, an extra thank you for the fieldwork help - though in hindsight, those 5 a.m. departures probably weren't strictly necessary.

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Family - if you’ve read this far, I’m impressed. Honestly, I doubt it (and for good reason: it’s boring). But anyway: Mum, Dad, Davide, Nonna Anna (yes, we’re still using the mugs!), and the rest - thank you. I may not be around all the time, but I know we’ll always be there when it matters.
Zii - as always, you’re the rocks I stand on, the giants that carry me. Thanks for being you. May distance stays just a number compared to our friendship. Davide, Matteo, Andrea, and Francesco, here’s to another 25 years!
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Finally, to no one’s surprise – Nora. Thanks for being you. I honestly don’t know how you put up with me on a daily basis; either you’re getting secretly paid to do it, or you’ve got the patience of a saint. Either way, I got lucky. I couldn’t ask for a better partner, for the little stuff, the big stuff, and everything in between. With you, even the impossible feels doable. You are my family, and I couldn’t be happier. If this is just the start, then the future is going to be pretty great, as long as you’re in it.

III

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Effect of Wood Ash, Lime, and Biochar on the Establishment and Early Growth of Poplars on Acidic Soil Conditions

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Abstract

Poplars are traditionally cultivated on arable land, but other land types, such as forested land and forested arable land, may also provide significant opportunities for poplar plantations without competing with food production. However, these sites often have suboptimal soil pH levels that hinder optimal poplar growth, highlighting the need for improved establishment methods to enhance both survival and growth. This study investigates the establishment and growth of poplars (*Populus trichocarpa* and their hybrids) at forest land and forested arable land after application of wood ash, lime, and biochar using three different application methods: (i) amendment spread on the soil (Surface), (ii) amendment mixed with the soil (Mixed), (iii) amendment placed on the planting spot (Spot). Our findings revealed that wood ash and lime application almost double growth compared to untreated plants, 3 years after planting, and that growth increased equally independently whether wood ash or lime was mixed with the soil or applied on the soil surface while Spot application method resulted in overall lower growth than the Mix and Surface method. In contrast, biochar application had a lower effect on tree growth compared to wood ash and lime. This study highlights the potential of using wood ash to improve poplar growth on sites with low soil pH and that application methods can be adapted for different site conditions, thereby supporting the early establishment of these fast-growing plantations in sites with suboptimal soil conditions.

Keywords *Populus* · *P. trichocarpa* · Poplar plantation · Forest land · Forest arable land · Soil amendment

Highlights

- Wood ash and lime application enhanced poplar growth in both forest and forested arable land.
- Wood ash enhanced growth in a wider soil pH range compared to lime.
- Biochar application had limited impact on early poplar growth.
- Application methods Mixed or Surface resulted in similar growth increment.
- Wood ash application on forested arable land shows potential for enhancing the establishment of poplar plantations in Sweden.

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Introduction

Transitioning to fossil-free and zero-carbon energy systems is essential for meeting climate goals and reducing CO_2 emissions. The European Commission has recommended afforestation of former agricultural lands as a sustainable land management practice to simultaneously contribute to CO_2 mitigation, biodiversity enhancement, and an increased supply of woody biomass [1]. This growing demand for bio-based resources is driven by the expanding production of existing products and the development of new bio-based materials, putting pressure on current biomass supplies which may fall short of future needs. One effective strategy to bridge this gap is to maximize biomass yield per unit area by planting fast-growing, early-successional tree species, such as *Populus*, combined with effective management practices over large areas.

In Sweden, approximately 500,000 hectares of arable land, 2.5 million hectares of forest land, and an additional 1.2 million hectares of arable land (forested arable land) that has transitioned to forested land over the past 70 years

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could be available for establishing *Populus* plantations [2, 3]. Forested arable land, while maintaining characteristics of high soil fertility and water-holding capacity both important for fast-growing broadleaf species, has often undergone soil acidification, especially following one 70–80 years long rotation with Norway spruce (*Picea abies* Karst) [4, 5]. Given the potential production of *Populus* plantations at these sites that can reach 6 Mg ha^{-1} $year^{-1}$, there is a significant incentive to investigate treatments that could enable poplar growth on sites with sub-optimal soil pH, especially considering that the usage of a fraction (25%) of these areas could supply up to 10 TWh of biomass annually without competing with food or feed production [2]. Furthermore, the increasing frequency of insect pests and storms over the past two decades has compelled foresters to consider alternatives to spruce at forest land and forested arable land.

Poplars (*Populus trichocarpa* Torr. & A.Gray ex Hook., *Populus maximowiczii* A.Henry and their hybrids) are known to be nutrient and water demanding and require a soil pH > 5 for optimal growth; below this, growth reductions are common due to nutrient limitations and increased susceptibility to aluminum (Al) toxicity [6–9]. Low soil pH can impair plant development in several ways, including increased mortality from high proton (H^+) levels, inhibited water uptake, and deficiencies in essential nutrients such as phosphorus (P) and calcium (Ca), as well as toxicities from increased availability of metal ions such as aluminum (Al), manganese (Mn), and magnesium (Mg) [10–14]. Specifically, soluble Al^{3+} ions are one of the main chemical constraints on plant growth in acidic soils by inhibiting root elongation [15, 16], altering ion fluxes, disrupting membrane channels, and interfering with nutrient uptake [17–21]. For poplars, Al^{3+} sensitivity has been suggested to be one of the factors limiting poplar establishment and growth in acidic conditions [9, 22, 23].

Application of lime or wood ash can increase soil pH [24–27]. Some studies show positive growth effects after liming [28–30] while other studies report neutral growth effects [22, 31, 32] and even negative effects [22, 24, 33]. Similarly, wood ash's effect on growth is variable, with studies reporting increased growth [34–40] but others reporting neutral or negative effects [26, 31, 41–43]. Besides increasing soil pH, liming and wood ash application can result in an addition of macro- and micronutrients. Liming primarily adds calcium (Ca) and magnesium (Mg) while wood ash supplies additional phosphorus (P) and potassium (K) [44]. Application of biochar can also affect plant growth by improving soil moisture retention, increasing nutrient availability, and reducing soil toxicity by adsorbing toxic ions like Al^{3+} [45–47] but similar to lime and wood ash, growth effects are variable with studies reporting positive [46, 48], neutral [49, 50], or negative effect [51]. As poplars rely on fast growth to establish, early access to soil water and nutrients is critical for newly planted seedlings [52, 53], with studies showing that root systems can extend over a meter during the first year [54]. As such, soil amendments aimed at improving soil proprieties must have a rapid effect to support the establishment and early growth phases for poplar seedlings. However, the amendment effect on plant growth is complex and varies based on factors such as soil proprieties, amendment composition, and application method, thus resulting in variable growth effects.

Despite studies on individual methods [23, 28, 30], limited research has directly compared different application methods to assess their impact on poplar growth in acidic soils on forest land and forested arable land. To address this knowledge gap, we conducted an experiment on forest land and forested arable land. The objectives of this study were to (1) evaluate the early growth response of *P. trichocarpa* and its hybrids to soil treatments with wood ash, lime, and biochar in forest and forested arable land and (2) examine the influence of different application methods of these amendments on the early growth and establishment of poplars, ultimately supporting high productivity and biomass supply on land unsuitable for food production.

Materials and Methods

Site Description and Climate Conditions

The experimental sites are located in southern Sweden (Fig. 1) and were established between 2019 and 2020. The experiment was placed at two site types: (i) forest land sites (For) with a continuation of forest coverage for more than 100 years and (ii) forested arable land sites (ArFor), i.e., former agricultural land planted with one rotation of Norway spruce that was grown for 40 to 70 years (Fig. 1). Prior to the experiment establishment, a homogeneous newly clear-felled area was selected at each site to undergo planting of the experiment. Temperature and precipitation were recorded at a local weather station within 10 km of the sites Table 1.

Plant Material

Plants were produced by first collecting dormant cuttings in February. These were thereafter stored at 4 °C until planting. In spring, i.e., April, cuttings were planted in containers 250 ml containing plant nursery soil mixture consisting of 83% peat, 5% clay, 7% gravel, 7% hydrograins, and N-P-K 11–5–8 plus micronutrients with a pH of 5.5–6.5 and grown to approximately a height of 40 cm and diameter of about 5 mm under field conditions. The plants were stored at + 2 °C during the following winter before planting in spring 2020. At the time of the planting, the poplar seedlings were 1 year old.

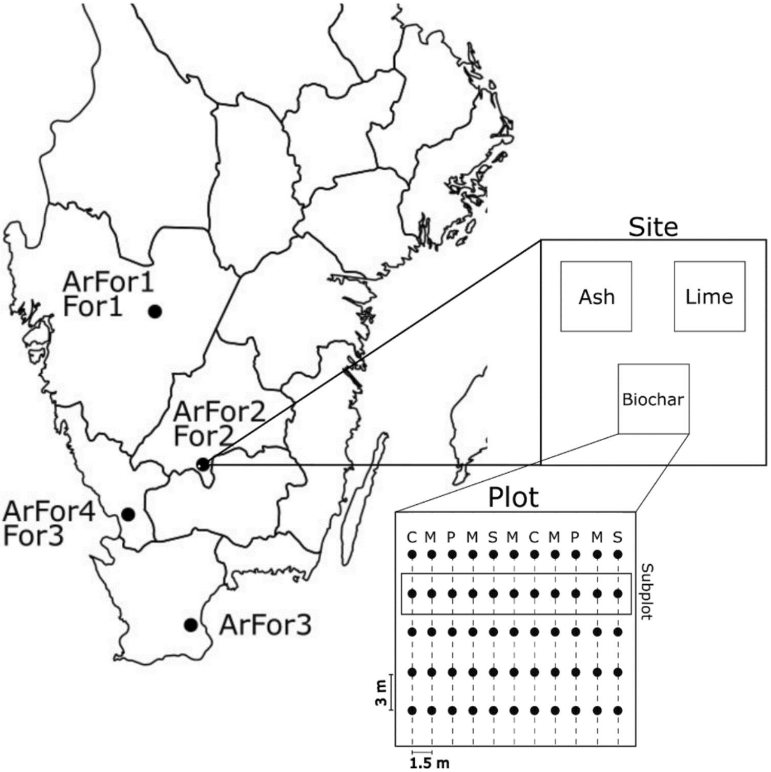

Fig. 1 Map of southern Sweden marked with the experimental sites and the experimental design used at all sites. Sites are marked as forested arable land (ArFor, i.e., former agricultural land planted with one rotation of Norway spruce that was grown from 40 to 70 years sites) and forest sites (For, i.e., used as forest land for more than 100 years). Note that ArFor1-For1, ArFor2-For2, and ArFor4-For3 are located less than 1 km from each other; thus, only one point represents two sites. Each site is divided in three plots (ash, lime, and biochar). Application methods are shown as mixed (M), surface (S), spot (P) and untreated, i.e., control (C) columns. Each planting position is shown with a filled circle. The spacing between the tree rows was 3 m while between plants was 1.5 m; the plot size was in total 18 × 18 m

Table 1 Description of experimental sites and their climatic conditions

Site	Latitude °N	Longitude °E	Precip, mm/year	Mean temp, °C	Site index
For1	58°27′12.8″N	13°38′41.8″E	740	7	G32
For2	57°00′38.4″N	14°22′16.7″E	780	6	T28
For3	56°42′03.6″N	13°05′21.7″E	920	5	G32
ArFor1	58°27′56.9″N	13°34′09.8″E	740	8	G32
ArFor2	57°02′07.5″N	14°20′10.7″E	780	6	G32
ArFor3	55°41′28.3″N	14°05′42.0″E	660	8	G36
ArFor4	56°39′45.6″N	13°03′57.0″E	920	5	G34

Site index (SI) corresponds to the dominant height of Norway spruce (G) or Scots Pine (*Pinus sylvestris* L.) (T) at an age of 100 years. Mean temperature is the yearly average temperature in °C since 2005. Precipitation represents the average yearly precipitation (mm) since 2005

At all sites, mechanical soil preparation in rows was performed using an excavator. The planted clones at site For1, For3, ArFor1, ArFor3, and ArFor4 were clone Androscoggin (*P. maximowiczii* × *P. trichocarpa*), clone Rochester (*P. trichocarpa* × *P. nigra*), clone 14 (*P. trichocarpa*), and OP42 (*P. maximowiczii* × *P. trichocarpa*), and at site For2 and ArFor2, SnowTiger® SLU clones "23.4," "26.1," "44.7," and "722.16" (all provenance hybrids within *P. trichocarpa*; [55]) were planted. In this study, the different *Populus* species and hybrids are referred to as poplar.

Experimental Design

At each site, plants were planted in plots treated with either ash (3 Mg ha^{-1}), lime (3 Mg ha^{-1}), or biochar (20 Mg ha^{-1}), as well as in untreated control plots. Within each plot, five subplots were designed, each containing three application methods:

(i) Mixing method (Mixed): where the amendment was mixed with the soil in a 1 × 1 m^2 to a depth of about 30 cm
(ii) Surface method (Surface): where the amendment was evenly applied to the soil surface 1 × 1 m

(iii) Planting spot method (Spot): where the amendment was applied in a 0.3-m diameter cylinder hole
(iv) Untreated (Control): no amendment was applied

The spacing between plants in each subplot was 1.5 × 3 m and all subplots were randomly distributed within the plots (Fig. 1). The experiment was fenced to prevent browsing damage and manually planted using a shovel. Within each treatment plot (wood ash, lime and biochar), 25 plants were treated using the Mix method, while 10 plants were treated with Surface and Spot methods, and 10 plants were designated as untreated Control.

At sites For1, For3, ArFor1, ArFor3, and ArFor4, the Mix-treated plots were planted with the clones (number of transplants under brackets): "OP42" (7), clone "Androscoggin" (6), clone "Rochester" (6), and clone "14" (6). For the Surface, Spot, and Control treatments, the planting configuration included clone "OP42" (3), clone "Androscoggin" (3), clone "Rochester" (2), and clone "14" (2). At sites For2 and ArFor2, the Mix-treated plots included clone "722.16" (7), clone "26.1" (6), clone "44.7" (6), and clone "23.4" (6). Similarly, for the Surface, Spot, and Control treatments, the planting scheme consisted of clone "722.16" (3), clone "26.1" (3), clone "44.7" (2), and clone "23.4" (2). More information about the clones deployed in the study can be found in supplement S3.

Lime, Wood Ash, and Biochar

The pulverized calcitic lime used was Ingaberga 0–0.02 mm, Nordkalk AB, Hässleholm Sweden, produced by grinding limestone to a particle size of 0–0.02 mm.

Biochar was produced by pyrolysis (750 °C) of barley and wheat seed residue pellets 4 × 20 mm in a Pyreg® pyrolysis unit. Wood ash was produced by combustion of forest residues, branches, and tops of *Pinus sylvestris* L. and *Picea abies* Karst in a commercial biomass boiler. The type of wood ash used in this study was 95% bottom and 5% fly ash. Samples of wood ash were analyzed at ALS Scandinavia AB, Luleå, Sweden, using analysis of metals in solid matrices with ICP-SFMS according to SS-EN ISO 17294–2:2023 and US EPA Method 200.8:1994 after digestion of samples according to S-PS49-FU. The chemical characteristics of the biochar used were analyzed by determination of selected elements by inductively coupled plasma optical emission spectrometry in accordance with DIN EN ISO 11885 (E22): 2009–09 and DIN 51732:2014–07. Analysis results of the wood ash, lime, and biochar are shown in Table 2.

Table 2 Elemental analysis of wood ash, lime, and biochar used in this study

Element/compound	Lime	Wood ash	Biochar
Bulk density (kg/m^3)	881	412	291
P (%)	0	3.6	16.5
Ca (%)	50.1	34.1	12.8
Mg (%)	0.5	8.6	6.9
Na (%)	0	0.5	0.8
K (%)	0	10.4	26.4
Zn (mg/kg)	0	1950	144
Fe (%)	0	1.4	0.9
Mn (%)	0	4.0	0.02
Si (%)	0	8.3	30.4
Cd (mg/kg)	0	22.2	< 0.02
Pb (mg/kg)	0	23.1	< 2
Cr (mg/kg)	0	542	5.0
Ni (mg/kg)	0	58.2	4.0
C (%)	0	48.2	78.3
N (%)	0	0.3	2.9
C/N	0	160.7	27.0
pH	12.3	12.1	10.1

% is shown as percentage of dry weight (DW)

Measurements and Soil Analyses

Survival, stem height, and root collar diameter (10 cm above the soil surface) were recorded at planting and after first, second, and third years of growth. To determine the effect on soil chemistry, 12 soil samples in untreated, ash, lime, and biochar (Mixed method) plots were sampled at a depth of 30 cm and pooled to generate one sample for each site. The samples were collected 3 years after application. Soil samples were analyzed at Eurofins Agro Testing Sweden AB in Kristianstad, Sweden, using ammonium lactate/acetic acid solution (the AL-Method) in accordance with the method SS 028310:1995–12 and by inductively coupled plasma optical emission spectrometry in accordance with the method ISO 11885:2009–09. The results are presented in Table 3.

Statistical Analysis

All data analyses were implemented in R version 4.4.1 [56]. To test the effect of soil amendments and their application method on tree growth (i.e., tree height and root collar diameter), we used linear mixed-effects models implemented in the "lme4" package [57]. Survival as a Boolean variable was tested using generalized linear mixed models implemented in the "glmmTMB" package [58]. The response variables tested were tree height, root collar diameter, and survival. Site type (For and ArFor), amendment (wood ash, lime, and biochar), application method (Mixed, Surface, Spot, and Untreated), and their interactions were set as fixed effects while site was treated as a random effect. To evaluate statistical differences among treatments, Tukey's HSD post hoc test, implemented in the "emmeans" R package [59] was used. A $p \leq 0.05$ was used as

Table 3 Analysis of the soil properties and elements content. Mean values across sites for soil chemistry parameters (pH, N, P, K, Ca, Mg, Mn, Cu, Fe, Zn, CEC, and BS) before and after treatments (biochar, lime, and ash) at forested arable land (ArFor) and forest land (For)

	Treatment	pH	N (mg/kg)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	Mn (mg/kg)	Cu (mg/kg)	Fe (mg/kg)	Zn (mg/kg)	CEC (meq/100 g)	BS (%)
ArFor	Untreated	4.9	19.9	1.7	1.8	16.8	1.2	9.3	0.2	213	2.4	13.7	5.1
	Biochar	5.5	3.8	3.3	7.7	37.4	4.3	21.8	0.6	260	2.9	15.1	14.8
	Lime	6.0	5.8	3.4	3.7	113	5.5	6.8	0.4	227	1.0	15.4	32.0
	Ash	5.8	2.5	4.8	6.7	76.9	8.3	55.5	0.7	234	4.8	15.3	29.8
For	Untreated	4.6	13.4	1.7	1.4	7.8	0.7	5.9	0.2	447	0.4	10.3	2.8
	Biochar	5.1	3.2	3.0	4.9	10.5	3.0	7.2	0.6	440	1.5	16.2	6.3
	Lime	5.0	5.0	2.9	3.7	19.5	4.0	8.8	0.5	550	1.9	16.5	9.2
	Ash	5.4	2.6	2.9	5.6	32.2	6.7	43.3	0.7	490	2.2	15.2	19.0

Untreated values represent soil chemistry in untreated plots, while biochar, lime, and ash values reflect post-treatment effects with the corresponding amendment. Parameters include pH, total nitrogen (N, mg/kg), phosphorus (P, mg/kg), potassium (K, mg/kg), calcium (Ca, mg/kg), magnesium (Mg, mg/kg), manganese (Mn, mg/kg), copper (Cu, mg/kg), iron (Fe, mg/kg), zinc (Zn, mg/kg), cation exchange capacity (CEC, meq/100 g), and base saturation (BS, %). Values for P, K, Ca, Mg, Mn, Cu, Fe, and Zn represent the plant available concentration

the cutoff for statistical significance. Residuals showed normal distributions with no high-leverage outliers using "DHARMa" package [60].

To analyze the effect of wood ash, lime, and biochar on tree height after three growing seasons in Mixed application method in relation to soil characteristics (pH, N, P, K, Al, Ca, and Mg), linear regression was used.

Results

Plant Survival

Three years after planting, plant survival was affected by wood ash, lime, or biochar and their application method (Table 4). On forest land (For), survival of plants treated with wood ash, lime, or biochar was found to be higher compared to untreated plants, varying between 68 and 97% depending on the application method. On forested arable land (ArFor), lime-treated plants displayed higher survival rates among all application methods compared to untreated plants while only wood ash and biochar with Mixed method resulted in increased plant survival compared to untreated plants. There were though no differences found for survival when wood ash and biochar were applied with Surface method (Table 4). These differences were not observed in the first 2 years after planting (Table 4).

Lime and Wood Ash Increased Tree Growth at Forest and Forested Arable Land

Across application methods, wood ash and lime increased tree growth at For and ArFor (Table 5). At For, tree heights on the ash-treated soil were 206%, 238%, and 227% of the heights of the untreated trees in the first, second, and third year after planting, respectively. At ArFor, the corresponding heights were 123%, 140%, and 148% of the untreated trees in years 1, 2, and 3, respectively.

Similar to tree heights, root collar diameters on ash-treated soil were 228%, 243%, and 267% of the diameters of the untreated trees after the first, second, and third year, respectively. At ArFor, the corresponding diameters in the first, second, and third year after planting were 131%, 148%, and 162%, respectively. There were differences between the treatments with wood ash being the most effective and biochar the least effective in increasing tree growth (i.e., height and diameters) the third year after planting at both For and ArFor (Table 5).

Mixing Wood Ash or Lime with the Soil or Applying the Amendment on the Soil Surface Increased Growth of Poplars Similarly

At the ArFor sites, ash-treated plants with the Mixed method resulted in plants reaching a mean height of

Table 4 Plant survival rates (%) in forest land (For) and forested arable land (ArFor) after application of wood ash, lime, or biochar using the application methods Mixed, Surface, and Spot

	Treatment	Method	Year one		SE		Year two		SE		Year three		SE	
For	Ash	Untreated	90.7	±	4.4	a	83.6	±	5.5	a	62.2	±	7.5	a
		Mixed	97.6	±	1.8	a	97.4	±	1.9	a	95.0	±	3.8	b
		Surface	100.0	±	0.0	a	96.0	±	3.3	a	96.9	±	7.6	b
		Spot	87.5	±	6.7	a	90.2	±	5.7	a	90.6	±	8.0	b
	Lime	Untreated	83.9	±	6.0	a	70.3	±	7.3	a	30.7	±	7.8	a
		Mixed	94.9	±	2.8	a	88.2	±	4.3	a	86.4	±	4.8	b
		Surface	96.7	±	3.2	a	96.8	±	3.3	a	87.7	±	6.4	b
		Spot	96.7	±	3.2	a	96.8	±	3.3	a	90.8	±	5.5	b
	Biochar	Untreated	88.8	±	4.9	a	83.6	±	5.5	a	31.0	±	7.8	a
		Mixed	87.2	±	4.9	a	85.6	±	4.8	a	68.7	±	7.4	b
		Surface	80.6	±	8.4	a	83.6	±	7.3	a	77.5	±	8.7	b
		Spot	93.7	±	4.7	a	90.2	±	5.7	a	80.8	±	8.0	b
ArFor	Ash	Untreated	90.3	±	3.9	a	74.8	±	6.0	a	56.5	±	7.5	a
		Mixed	93.6	±	2.7	a	89.2	±	3.4	b	87.3	±	3.8	b
		Surface	89.7	±	4.7	a	81.8	±	6.0	ab	71.8	±	7.6	ab
		Spot	91.3	±	4.2	a	72.0	±	7.4	a	67.8	±	8.0	a
	Lime	Untreated	89.6	±	4.1	a	80.8	±	5.2	a	61.5	±	7.3	a
		Mixed	97.6	±	1.5	a	90.7	±	3.1	a	84.1	±	5.7	b
		Surface	94.9	±	3.1	a	94.6	±	3.2	a	86.6	±	4.0	b
		Spot	89.7	±	4.8	a	87.3	±	5.0	a	94.1	±	3.5	b
	Biochar	Untreated	94.3	±	2.8	a	80.6	±	5.2	a	64.1	±	7.1	a
		Mixed	96.1	±	2.0	a	88.0	±	3.6	a	82.9	±	4.6	b
		Surface	96.7	±	2.5	a	90.8	±	4.2	a	79.5	±	6.7	ab
		Spot	98.4	±	1.7	a	96.4	±	2.6	a	85.7	±	5.6	ab

Data shown represent survival rates in % across experimental sites. Letters represent statistical differences ($p \leq 0.05$) between application methods within the same type of amendment and site type

225 cm, followed by Surface (200 cm), Spot (160 cm), and untreated plants (140 cm) (Fig. 2A) with no differences between Mixed and Surface application methods (Fig. 2A). This was also found for diameter growth at For and ArFor sites, with the Surface method resulting in similar diameters as Mixed (Fig. 3A and D). At the For sites, ash application resulted in similar height growth increment between Mixed and Surface application methods with plants reaching mean heights of 200 cm and 180 cm, respectively (Fig. 2D).

For lime-treated plants, the effect of different application methods followed a similar pattern, with Mixed method reaching an average height of 170 cm followed by Surface (165 cm), Spot (160 cm), and untreated (130 cm) (Fig. 2B) with no significant differences between Mixed and Surface (Fig. 2B). At For sites, application of lime resulted in no differences between the application methods, all reaching a height of 145–148 cm (Fig. 2E) but compared to untreated plants, height growth was increased (Fig. 2E). Diameter growth with Mixed and Surface resulted in similar increments (Fig. 3B and E).

In conclusion, amendments using Mixed and Surface application methods were similarly effective in increasing tree growth at For and ArFor.

At ArFor sites, all application methods with biochar did not alter height and diameter (Figs. 2C and 3C). In For sites, untreated plants reached a mean height of 65 cm and 6 mm diameters while treated plants had heights of roughly 95 cm to 100 cm and 11 mm to 15 mm in diameter. However, no significant differences ($p > 0.05$) were detected (Figs. 2F and 3F) for all the application methods.

Impact of Treatment on Plant Height at Different Soil Characteristics Levels

The ash-treated plants consistently outperformed the untreated plants across all pH, aluminum (Al), and potassium (K) levels, achieving heights exceeding 200 cm, whereas the untreated plants only reached 100–110 cm (Fig. 4A, J, and M). Phosphorus (P) content in the soil had a stronger positive impact on untreated plants ($R = 0.41$, $p = 0.004$) than on treated plants ($R = 0.18$, $p = 0.023$),

Table 5 Plant height (cm) and root collar diameter (mm) after the application of wood ash, lime, and biochar in forest land (For) and forested arable land (ArFor)

	Treatment	Year one								Year two			
		Height		SE		Diam		SE		Height		SE	
For	Untreated	35.8	±	7.0	a	2.8	±	0.3	a	56.6	±	5.2	a
	Biochar	40.9	±	6.8	a	3.7	±	0.4	b	73.1	±	4.6	b
	Lime	53.8	±	6.8	b	4.5	±	0.5	c	94.6	±	4.6	c
	Ash	73.9	±	6.8	c	6.4	±	0.7	d	134.5	±	4.5	d
ArFor	Untreated	61.6	±	6.1	a	4.9	±	0.5	a	99.2	±	4.8	a
	Biochar	67.2	±	5.9	a	5.7	±	0.5	b	112.2	±	4.0	ab
	Lime	69.1	±	5.9	ab	5.7	±	0.5	b	113.8	±	4.0	b
	Ash	75.7	±	5.9	b	6.4	±	0.6	c	139.2	±	4.1	c
		Year two				Year three							
	Treatment	Diam		SE		Height		SE		Diam		SE	
For	Untreated	6.0	±	0.5	a	85.8	±	11.5	a	8.1	±	0.7	a
	Biochar	8.3	±	0.6	b	105.2	±	9.8	b	11.1	±	0.8	b
	Lime	10.3	±	0.7	c	140.8	±	9.5	c	14.8	±	1.1	c
	Ash	14.6	±	1.0	d	194.5	±	9.3	a	21.6	±	1.6	d
ArFo	Untreated	8.6	±	0.6	a	145.8	±	9.5	a	12.1	±	0.9	a
	Biochar	10.2	±	0.6	ab	173.4	±	8.4	b	15.3	±	1.0	b
	Lime	9.9	±	0.6	b	181.3	±	8.2	b	15.5	±	1.0	b
	Ash	12.7	±	0.8	c	215.9	±	8.2	c	19.6	±	1.3	c

Data shown represent mean height and diameter of trees in each of the three years after planting. Letters represent statistical differences ($p \leq 0.05$) between treatments within the same site type

with ash-treated plants reaching 200 cm height at low P concentrations while untreated plants reached 100 cm at the same P level (Fig. 4G). Additionally, ash-treated plants performed better at low calcium (Ca) and magnesium (Mg) levels but similarly to untreated at higher concentrations (Fig. 4P and S).

Lime application was most effective under low pH and phosphorus (P) concentrations, with treated plants reaching 160 cm compared to 90 cm for untreated plants (Fig. 4B and H). However, at higher pH and P levels, both lime-treated and untreated plants showed similar heights (Fig. 4B and H). Potassium (K) had a similar impact on both lime-treated and untreated plants ($R = 0.35$, $p < 0.001$ and $R = 0.28$, $p = 0.092$, respectively), but treated plants consistently grew taller across all K levels (Fig. 4K). Aluminum (Al) negatively affected treated plants ($R = -0.21$, $p = 0.012$), resulting in 180 cm heights at lower Al levels and 140 cm at higher levels, similar to untreated plants (Fig. 4N). Lime-treated plants performed better under low calcium (Ca) and magnesium (Mg) levels but similarly to untreated plants at higher levels (Fig. 4Q and T). Nitrogen (N) positively influenced growth in both lime-treated and untreated plants ($R = 0.32$, $p < 0.001$ and $R = 0.39$, $p = 0.018$, respectively) (Fig. 4E).

In contrast to wood ash and lime, biochar application did not influence growth performance of poplars for any soil parameters analyzed (Fig. 4C, F, I, L, O, R, and U).

Discussion

Poplar plantations have traditionally been established on arable or agricultural land [61]. However, forested and forested arable lands present a significant, largely untapped potential for poplar cultivation, with several million hectares available in Sweden [2, 3]. Despite this, these areas have not been planted as they often have acidic soil conditions that can negatively impact poplar growth [5, 28, 62]. Our findings reveal that soil amendments such as wood ash and lime—and to a lesser extent, biochar—effectively enhance growth on both forest and forested arable sites (Table 5, Figs. 2 and 3), where soils tend to be acidic (Table 3).

These results are consistent with previous research showing growth benefits from wood ash, lime, and biochar treatments on tree species, including poplars, in acidic conditions [28, 30, 34, 63–66]. Specifically, wood ash and lime application almost doubled the growth of poplars compared to untreated, suggesting that when soil

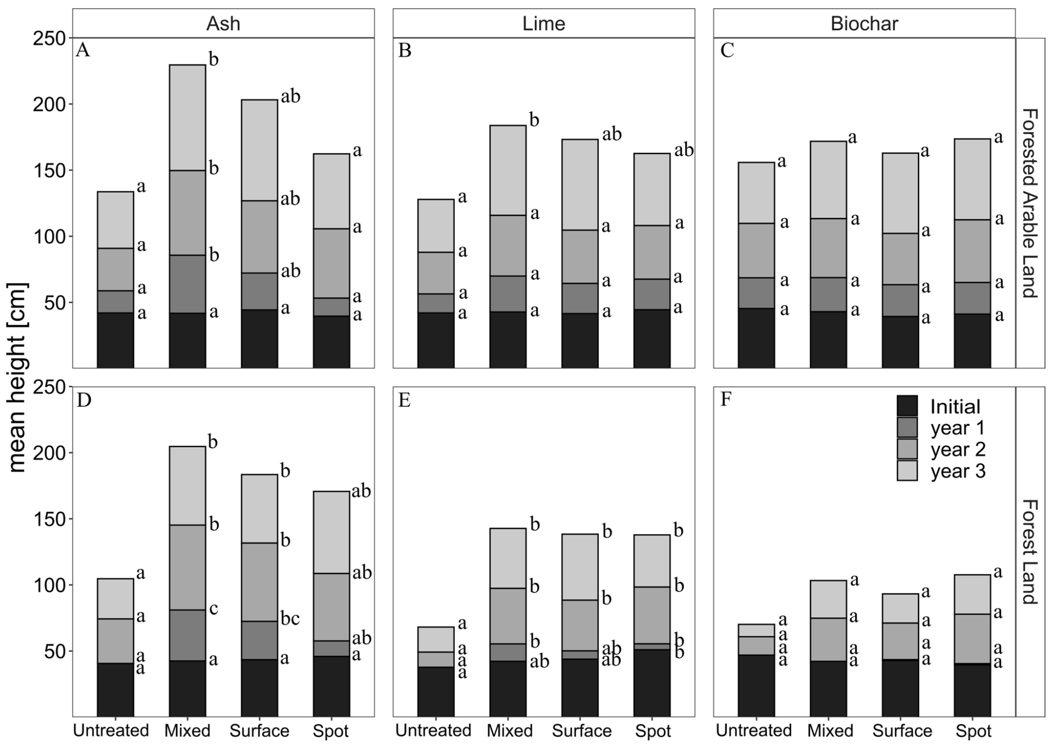

Fig. 2 Height growth at forested arable land (ArFor) **A** to **C** and forest land (For) **D** to **F**. Application of ash are shown in **A** and **D**, lime **B** and **E,** and biochar **C** and **F**. Letters indicate significant differences ($p \leq 0.05$) between the treatments within each year. Note that if a bar is missing, the corresponding yearly growth is too low to be shown

pH is sub-optimal for poplars, applying wood ash or lime may foster rapid growth and improve establishment.

Previous studies have found positive growth effects from biochar application on conifers, such as Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.), as well as on broadleaf species, including poplars, aspens (*Populus tremula* and *Populus tremuloides*), and silver birch (*Betula pendula*) [48, 67–70]. On the other hand, in other studies, biochar has shown limited growth effects on species such as poplar, alder, and willow [71, 72]. Ultimately, the growth impact of biochar varies heavily depending on application dosage, soil proprieties, and the biomass origin used for biochar production, highlighting the complex interactions between biochar type, soil properties, and plant growth [73, 74]. In this study, biochar derived from straw residues was applied, which may have been less effective in promoting poplar growth. Additionally, previous studies suggest that biochar's impact is enhanced when nutrient supplements are included [75–78], a factor not addressed in our experiment. These factors combined likely reduced the biochar's growth-promoting effects (Figs. 2C and F and 3C and F).

Previous studies have generally focused on either surface applications [28, 34, 79] or mixing the amendments into the soil during soil preparation [23, 30]. Interestingly, our results show only minor differences in growth and survival between the Mixed and Surface application methods (Tables 4 and 5, Figs. 2 and 3). Given prior research suggesting that surface applications might act more gradually on soil pH [26, 34] whereas mixing can yield immediate changes, one might anticipate greater effectiveness from the Mixed method. However, our findings indicate that both application methods can support poplar establishment at sites with sub-optimal conditions.

There are advantages and disadvantages associated with each of these methods. The Mixed method is more labor-intensive and requires application during soil preparation using specialized machinery to ensure cost efficiency. For this reason, technical development that integrates soil preparation with lime or wood ash application needs to be

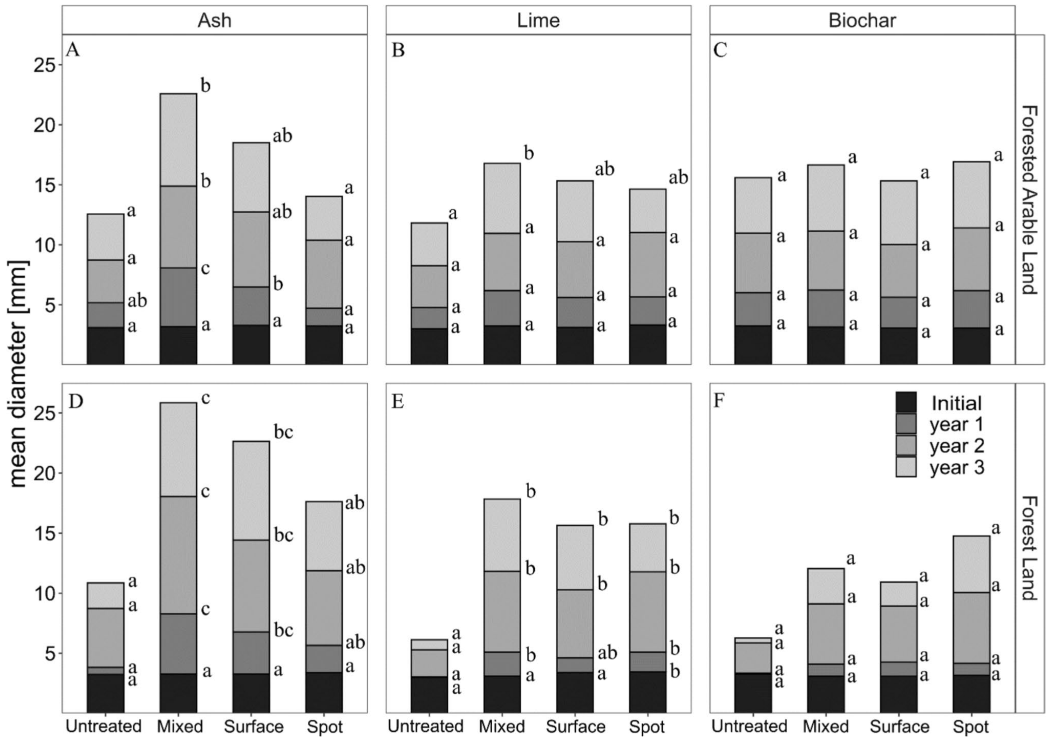

Fig. 3 Diameter growth at forested arable land (ArFor) **A** to **C** and forest land (For) **D** to **F**. Application of ash are shown in **A** and **D**, lime **B** and **E**, and biochar **C** and **F**. Letters indicate significant differences ($p \leq 0.05$) between the treatments within each year. Note that if a bar is missing, the corresponding yearly growth is too low to be shown

implemented. However, this method would require only one visit to the site. Conversely, the Surface method can utilize existing technology for application but currently requires two types of machinery: one for soil preparation and another for wood ash or lime application. An additional advantage of the Surface method is its ability to treat the entire planting area even at later stages of the rotation period, while the Mixed method can be applied only before planting. Moreover, the Surface method may be more versatile in treating sites with stones, potentially expanding areas suitable for poplar plantations compared to the Mixed method, which may be limited by its inefficiency in mixing wood ash or lime into soils containing large stones. Furthermore, advancements in drone applications within the agriculture and forestry fields might provide a low-effort and cost-effective way to apply wood ash or lime on the surface of the stands [80, 81].

Changes in soil pH are closely connected to the availability of macro- and micronutrients [82–84] but wood ash and lime can also influence soil fertility by addition of nutrients. There are though differences between the two compounds. Lime primarily adds calcium (Ca) and magnesium (Mg), whereas wood ash also provides phosphorus (P) and potassium (K), and micronutrients manganese (Mn), copper (Cu), molybdenum (Mo), and nickel (Ni) (Table 2). Indeed, at both our experimental site types (forest and forested arable sites), wood ash application increased P, K, Ca, Mg, Mn, and Zn levels and soil pH (Table 3), a result consistent with other studies [27, 39, 44, 85–87]. In fact, we do observe a higher growth with wood ash and that its effect spanned a broader pH and soil chemistry ranges (Fig. 4) indicating that these changes could be the reasons for wood ash increasing tree growth of poplars. It is important to note, however, that the growth effects of wood ash can vary considerably due to its variable composition [27, 88].

Low soil pH can impede plant growth by increasing the concentration of toxic metal ions, leading to stunted growth and plant mortality. Therefore, increasing soil pH through lime or wood ash application decreases the solubility of aluminum (Al^{3+}) and manganese (Mn^{3+}) ions, which are known

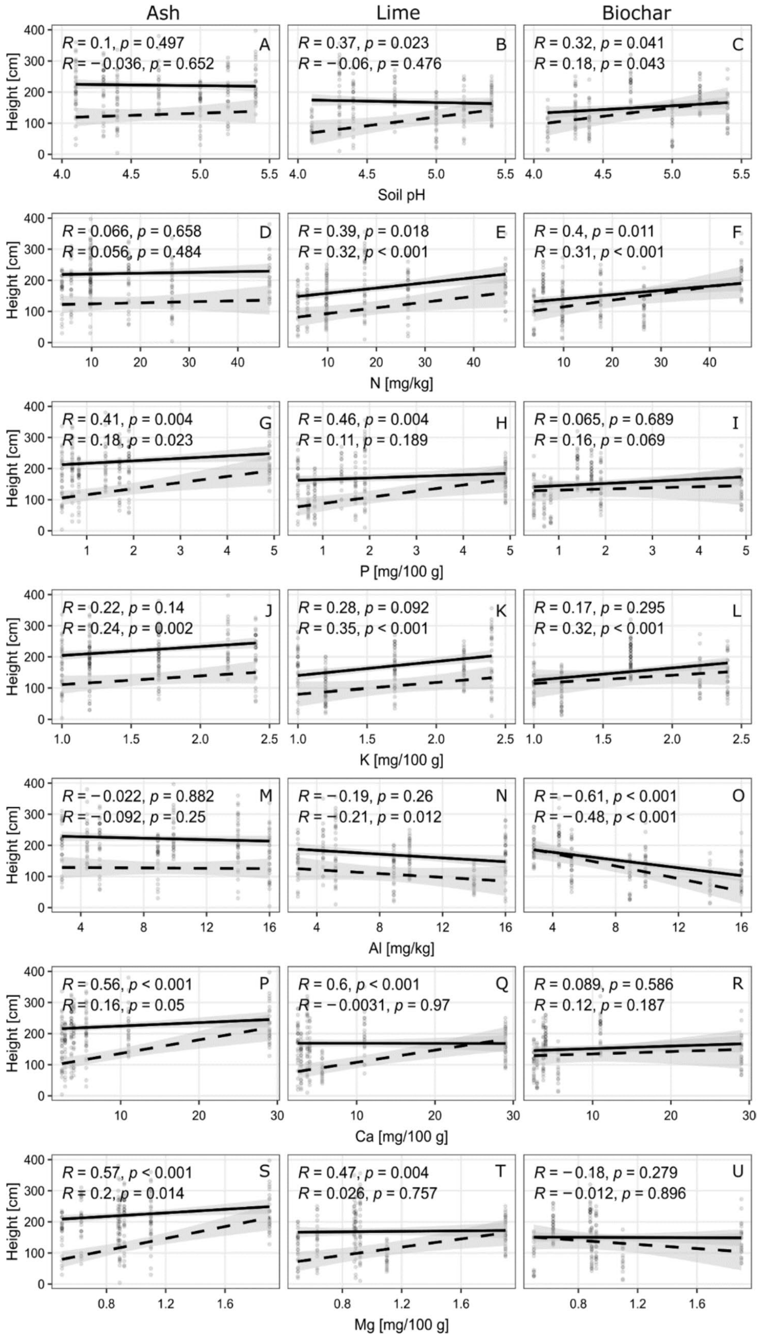

Fig. 4 Linear regression of tree height after three growing seasons vs. soil proprieties. A–**C** Soil pH with plants treated with **A** wood ash, **B** lime, and **C** biochar. **D**–**F** Total nitrogen (N) with plants treated with **D** wood ash, **E** lime, and **F** biochar. **G**–**I** Phosphorus (P) with plants treated with **G** wood ash, **H** lime, and **I** biochar. **J**–**L** potassium (K) with plants treated with **J** wood ash, **K** lime, and **L** biochar. **M**–**O** Aluminum (Al) with plants treated with **M** wood ash, **N** lime, and **O** biochar. **P**–**R** Calcium (Ca) with plants treated with **P** wood ash, **Q** lime, and **R** biochar. **S**–**U** Magnesium (Mg) with plants treated with **S** wood ash, **T** lime, and **U** biochar. The solid line represents plants treated with the respective soil amendment by the Mixed method, while the dashed line represents untreated plants. The *R*-value displayed at the top corresponds to the treated poplars (solid line), whereas the lower *R*-value represents the untreated poplars (dashed line). Confidence bands represent a 95% confidence interval

to inhibit root and shoot growth and increase mortality, particularly in Al^{3+} sensitive species like poplars [9, 89–92]. This toxicity reduction likely contributed to the improved growth we observed following lime and wood ash applications (Table 5, Figs. 2, 3, and 4).

Thus, the observed growth differences between wood ash and lime in our study likely originate from the combined effects of improved nutrient availability, nutrient supplementation, and the reduction of toxic metal ions, particularly crucial for early root development that has been shown to be of most importance for seedling establishment [52, 93]. While our study demonstrated elevated soil cation levels and base saturation (BS) after wood ash application (Table 3), the design did not allow us to determine the dominant factor driving growth improvements in poplar plantations on forest and forested arable land.

In our study, biochar showed a neutral (Figs. 2, 3, and 4) or positive (Table 5) effect on growth, though its increase was less pronounced than that observed with wood ash and lime. Biochar enhances plant growth by improving soil moisture retention and nutrient availability through reduced soil bulk density, increased fungal and microbial activity, and nutrient mineralization, while also mitigating toxic metal ion availability [45–47, 66, 94]. However, biochar has a longer residence time in soil compared to wood ash or lime, suggesting that while it has a slower direct impact on soil properties, its soil-improving effects may persist for decades or even centuries [95–97]. Given the rapid establishment needs of poplars, immediate soil condition changes are essential for optimal growth, especially in the early stages. The limited growth observed in our study suggests that biochar might not alter soil conditions quickly enough to benefit poplar seedlings within the timeframe of the study.

It should be noted that our soil analysis was designed to address spatial variability in soil properties within site [98, 99]. To account for this, our experiment incorporated multiple sampling points within each plot, thereby improving the reliability of the soil analyses. However, as the sampling was conducted 3 years after planting, potential temporal fluctuations in soil properties before and after treatments could not be assessed. Nevertheless, Simard et al. [100] found only minor changes in soil pH 2 years after clear-cutting, suggesting that temporal variations in soil pH may be relatively limited over comparable time periods.

In Sweden, poplar plantations on forested arable land are estimated to yield 4.5–6 Mg DW ha^{-1} $year^{-1}$ [2, 101] roughly 20% lower than those on arable land, where production averages around 8.4 Mg DW ha^{-1} $year^{-1}$. Our findings indicate that wood ash application can improve establishment and thus potentially increase biomass yields narrowing this production gap. Reduced mortality rates and improved growth in the early rotation phase are likely to contribute to higher biomass production at later stages, especially considering poplar need for rapid early growth to effectively establish, avoid competition, and withstand browsing pressure as a nutrient and water-demanding, pioneer species [61, 102]. However, our study covers only the first 3 years of the rotation period, leaving uncertainties regarding the long-term impact on total biomass production.

The establishment of large-scale poplar plantations on forested arable or forest land may face some regulatory constraints. For instance, Forest Stewardship Council (FSC) regulations limit the establishment of non-native species, like poplars, to 5% of forest land in Sweden. However, FSC guidelines permit non-native species to replace forest plantations, possibly classifying forested arable land as plantation forestry and thus allowing for poplar cultivation. Additionally, recent governmental recommendations in Sweden support planting broad-leaved species on such lands [103]. By contrast, poplar plantations on arable land are classified as energy crops and are not subject to FSC land-use restrictions, as these apply solely to forest lands.

This study's findings underscore the potential of wood ash as an amendment to increase biomass production from poplars on forested arable land, albeit with some regulatory and application considerations for maximizing its benefits.

Conclusions

Our investigation on the effects of wood ash, lime, and biochar applications on poplar growth at forested and forested arable sites offers valuable insights into how to enhance the establishment and the early growth of hybrid poplars in acidic soils in the temperate climate of northern Europe.

The results underscore wood ash's potential to improve poplar growth comparably to lime, suggesting a sustainable alternative for promoting poplar plantations on suboptimal sites. Furthermore, our findings indicate that applying wood ash or lime to the soil surface is as effective in promoting tree growth as mixing them into the soil. Such insights are critical for developing sustainable management practices for poplar plantations, contributing to biomass production and maximizing land utilization in areas unsuitable for food or feed production. Additionally, these results provide foundation for further research aimed at understanding the mechanisms underlying the impact of wood ash on poplar growth in suboptimal soil conditions.

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Author Contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Luca Muraro and Henrik Böhlenius. The first draft of the manuscript was written by Luca Muraro and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during and/or analyzed during the current study are available in the supplementary material (S4).

Declarations

Competing Interests The authors declare no competing interests.

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Swedish forestry seeks diversification with fast-growing broadleaves, but poplar establishment on acidic soils is limited by aluminium (Al) toxicity. This thesis combines field trials, clonal screening, soil amendments, and a systematic review to address these barriers. Results show large genotypic variation in Al tolerance, with tolerant clones identified through a Composite Tolerance Index. Wood ash most consistently improved survival and growth across sites. Together, genetic selection and targeted soil amendments enable broader deployment of poplars in sustainable forestry.

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