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Early establishment of fast-growing tree species on forest land and forested arable land in southern Sweden: Implications for forest diversification

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ABSTRACT

Climate change and pest outbreaks are increasingly threatening conifer-dominated forests in Northern Europe, highlighting the need for greater species diversity to improve resilience. This study assessed early establishment success of six tree species: European aspen (*Populus tremula*), hybrid aspen (*P. tremula* × *P. tremuloides*), silver birch (*Betula pendula*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and hybrid poplar (*P. trichocarpa* × *P. maximowiczii*), across seven sites in southern Sweden. Sites were categorized as either forest land (continuous forest cover >100 years) or forested arable land (former arable land afforested with Norway spruce for 40–70 years). Over three years, we monitored survival, height, and diameter growth. All experimental sites were fenced to exclude browsing. Wood ash was applied to a subset of hybrid poplars to assess its effect on establishment in acidic soils. Our results showed that hybrid aspen, birch, and European aspen had high survival and growth on forest land. On forested arable land, untreated Norway spruce, Scots pine, and hybrid poplar showed low survival, likely due to competition from dense vegetation. However, ash-treated poplar improved survival to approximately 80% and showed strong growth on forested arable sites. Principal Component Analysis indicated overall higher establishment success on forest land for most species, whereas hybrid poplar performed similarly on forest and forested arable land when wood ash was applied. These findings underscore the importance of matching species to site conditions during early establishment and provide empirical evidence to inform species selection for forest regeneration under similar site conditions in southern Sweden.

1. Introduction

Woody biomass from forests represents a key renewable resource in Europe, supporting both material production and energy supply while contributing to climate change mitigation and serving as a sustainable raw material that can replace fossil-based industries (Berndes et al., 2016; Egnell, 2011; Pelkonen et al., 2014). The average biomass utilization in Europe is estimated at 481 Mm^3 u.b. (million cubic meter under bark) per year (Mubareka et al., 2025). In several countries, forests and their products play a central role as renewable energy resources and as a key component of the national economy. Sweden, for example, accounts for just 1% of the world's commercial forest area yet contributes about 10% of the global trade in sawn wood, pulp, and paper (Kumar et al., 2021). This performance is driven by the industrial use of 23 million ha of productive forest, with forest-based products contributing around 10% of the country's total export value (Sandberg et al., 2014).

In Sweden, forestry depends heavily on two coniferous species, Norway spruce (*Picea abies* H. Karst) and Scots pine (*Pinus sylvestris* L.), which together make up roughly 80% of the total standing timber volume in Sweden (Skogsdata, 2025). While these species have traditionally been cultivated successfully, they are now increasingly vulnerable to climate-related stressors such as storm damage and pest outbreaks resulting in reduced growth and increased mortality (Aldea et al., 2024; Aldea et al., 2022; Schlyter et al., 2006). For instance, bark beetle infestations following the 2018 drought resulted in the loss of 118 Mm^3 of Norway spruce in Scandinavia and central Europe (Gohli et al., 2024; Kärvemo et al., 2023; Wulff and Roberge, 2021), and a 2023 outbreak in Germany destroyed 18 Mm^3 of Norway spruce forest. Given the ecological and economic importance of these species (Kapeller et al.,

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2017; Kellomäki et al., 2018), securing future wood supply under changing climate conditions has become a critical challenge.

One promising option to increase forest resilience is to diversify tree species selection across stands and landscapes based on species-specific site requirements, thereby reducing reliance on a limited number of dominant species and supporting long-term productivity (Mina et al., 2022; Pretzsch et al., 2014; Sebald et al., 2021). Tree species differ markedly in their ecological niches and establishment strategies; for example, Norway spruce is shade-tolerant and prefers fertile, moist but well-drained soils, whereas Scots pine is light-demanding and can tolerate a broader range of site conditions (Nilsson, 2020). Such differences in species ecology underline the importance of matching species to site conditions during the regeneration phase.

Beyond ensuring wood supply, diversification also has important ecological implications. Increasing tree species diversity at the landscape level creates a wider range of structural and compositional habitats, supporting higher biodiversity across multiple taxa, including understory plants, invertebrates, birds, and soil organisms (Brockerhoff et al., 2008; Felton et al., 2010; Gamfeldt et al., 2013). By increasing the number of ecological niches and functional traits across forest landscapes, a more diverse species pool can promote ecosystem multifunctionality and resilience to stressors (Bauhus et al., 2017). Broadleaved species such as birch and aspen are particularly valuable, as they provide light heterogeneity, deadwood, and cavities that serve as critical habitats for many red-listed species, i.e. species classified as threatened or near-threatened according to national or international Red List assessments (Kouki et al., 2001; Roberge and Angelstam, 2006). From a management perspective, deploying a broader range of tree species across regeneration areas can therefore contribute to biodiversity conservation and the maintenance of ecosystem services, even when species are established in monocultures at the stand level.

Despite their ecological value, native broadleaved species such as birch (*Betula pendula* Roth and *Betula pubescens* Ehrh) and Eurasian aspen (*Populus tremula* L.) have historically been underutilized in Northern European forestry. In Sweden, birch is the third most common tree genus, accounting for 13.1% of the standing volume, while aspen represents only 1% (Skogsdata, 2025). Both species often regenerate naturally on disturbed or recently harvested sites (Myking et al., 2011; Tiebel et al., 2020) with, well-drained, slightly acidic soils (Hynynen et al., 2010; Kivinen et al., 2020). However, management practices (such as complete removal during thinning and pre-commercial thinning), ungulate browsing - especially on aspen - and conifer-focused revenue models have limited their regeneration (Edenius et al., 2011). While birch planting is well-documented (Hynynen et al., 2010; Johansson, 2007; Karlsson, 2002; Niemistoö, 1995), the establishment of aspen, particularly through planting, remains insufficiently studied.

Beyond native species, non-native fast-growing broadleaved species offer opportunities for increasing productivity and biomass yield. Hybrid aspen (*Populus tremula* × *Populus tremuloides* Michx), a cross between Eurasian and North American aspen, has been tested in Northern Europe since the 1950s and has shown high growth potential across a range of sites, including both former agricultural and forest land (Fahlvik and Böhlenius, 2025; Ilstedt and Gullberg, 1993; Rytter and Stener, 2014; Stener and Karlsson, 2004; Stener and Westin, 2017). Hybrid poplar (*Populus trichocarpa* Torr. & A.Gray ex Hook. × *Populus maximowiczii* A.Henry) also demonstrates fast growth on former agricultural land (Böhlenius et al., 2023; Christersson, 2010) but has more specific site demands, requiring fertile soils and a soil pH above 5 for optimal performance (Bergstedt, 1981; Jobling, 1990; Rytter and Lutter, 2020). On sites with acidic soils (pH < 5), wood ash or lime amendments can improve establishment and early growth (Böhlenius et al., 2020; Bona et al., 2008; Muraro et al., 2025). Both hybrid species are pioneer species and offer rapid biomass accumulation and shorter rotation periods, making them attractive for industrial wood production and carbon sequestration (Castaño-Santamaría et al., 2013; Rytter et al., 2013; Tullus et al., 2012).

In Sweden, most land available for plantation forestry lies within the hemiboreal and boreal zones, where podzolic soils tend to be acidic and low in nutrients (Falkengren-Grerup, 1987; Lundström, 1993). However, approximately 1.2 million ha of former arable land have been afforested with Norway spruce over the past 70 years, and these soils may retain higher nutrient availability and water-holding capacity compared with long-established forest soils, making them potentially well-suited for establishing fast-growing species. Nevertheless, soil acidification resulting from the previous Norway spruce rotation (Iwald, 2016; Pallant and Riha, 1990), as well as dense seed banks and competitive vegetation associated with agricultural legacy, may present establishment challenges for some species. Such legacy effects can influence recruitment and vegetation dynamics for decades after afforestation, as soil seed bank composition may retain signatures of past land use (Koyama and Uchida, 2022).

The post-harvest regeneration phase is a critical window for implementing species diversification. Decisions made during the establishment phase of a stand largely determine the long-term productivity, vitality, and economic returns of a stand (Grossnickle, 2005; Grossnickle and MacDonald, 2017; Margolis and Brand, 1990). Thus, the selection of tree species must be carefully matched to site-specific conditions, including soil fertility, acidity, and land-use history. Despite its importance, there is a lack of comparative data on the early performance of different tree species across contrasting site types, particularly in forest landscapes of the temperate–boreal transition zone.

While long-term climate resilience depends on physiological and ecological traits that are not directly assessed here, successful early establishment represents a necessary prerequisite for forest regeneration under changing environmental conditions. The species included in this study differ in regeneration strategies, growth rates, and sensitivity to site-related constraints such as soil acidity, nutrient availability, and competition. Evaluating early survival and growth across contrasting land-use histories therefore provides a first filter for resilience-oriented species selection, even though it does not directly quantify long-term climate tolerance. This study aims to address that knowledge gap by assessing how land-use history and soil properties, especially fertility and pH, affect establishment success and height and diameter early growth in six tree species: European aspen, hybrid aspen, silver birch, Norway spruce, Scots pine, and hybrid poplar. The study compares performance on forest land and forested arable land (former arable land planted with one Norway spruce rotation). By conducting trials under controlled pedoclimatic conditions and using high-quality plant material, this work provides insights into the suitability of different species for future resilient and productive forestry in northern Europe.

2. Materials and methods

2.1. Experimental sites description and experimental design

The study was conducted in seven experimental sites established between 2019 and 2020 in southern Sweden across two site types: (*i*) forest land (For), with uninterrupted forest cover exceeding 100 years, and (*ii*) forested arable land (ArFor), former agricultural land converted to Norway spruce forest maintained for 40–70 years (Fig. 1). Notably, specific site pairs (For1/For2, ArFor1/For3, and ArFor2/For4) are located within 1 km of each other (Fig. 1). At each site, a uniformly clear-felled area was designated for experimental plots. Six plots were established per site with a size of 18x18m, each assigned to one of six tree species: European aspen (also referred as aspen), hybrid aspen, silver birch, Norway spruce, Scots pine and hybrid poplar (from now referred as poplars). All the plots, apart from the poplar ones, contained 50 plants with spacing 3 × 1.5 m (Fig. 1).

Poplar plots were part of a parallel experiment established at a higher initial planting density (1.5 × 1.5 m). For the present study, only every second row and every second tree within rows were included, corresponding to an analysed tree distance of 3 × 3 m. This subsampling

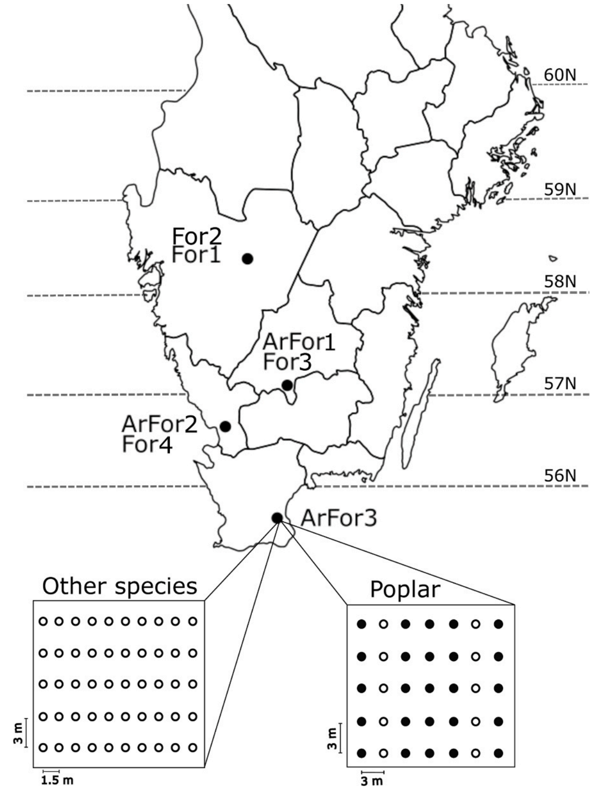

Fig. 1. Map of southern Sweden showing the location of the experimental sites and their shared experimental design. Sites were categorized into two types: forested arable land (ArFor), former agricultural land converted to Norway spruce plantations maintained for 40–70 years, and forest land (For), with more than 100 years of continuous forest cover. Specific site pairs (For1/For2, ArFor1/For3, and ArFor2/For4) are located within 1 km of each other and are therefore represented by a single map marker. At each site, six species-specific plots were established following the same layout. Planting positions without wood ash are indicated by hollow circles, while filled circles represent ash-treated poplar plants. For all species except poplar, planting spacing was 3.0 × 1.5 m. Poplar plots originate from a parallel experiment established at 1.5 × 1.5 m spacing; a systematic subsampling scheme was applied for the present study, corresponding to an analysed tree distance of 3.0 × 3.0 m for the poplar trees included in the analyses. Lines indicate latitude.

Table 1
Description of experimental sites and their climatic conditions during the experimental period.

Site	Latitude °N	Longitude °E	Mean annual precip, mm/year*	Mean annual temp, °C	Site index*
For1	58°27'12.8"N	13°38'41.8"E	760	8.1	G32
For2	58°27'56.9"N	13°34'09.8"E	750	8.2	G32
For3	57°00'38.4"N	14°22'16.7"E	880	7.6	T28
For4	56°42'03.6"N	13°05'21.7"E	1215	8.8	G32
ArFor1	57°02'07.5"N	14°20'10.7"E	875	7.8	G32
ArFor2	56°39'45.6"N	13°03'57.0"E	1145	8.9	G34
ArFor3	55°41′28.3″N	14°05′42.0″E	840	9.0	G36

* : Mean annual precipitation (mm) and temperature (°C) represent averages for the experimental period (2019–2022 or 2020–2023, depending on site) derived from gridded climate data PTHBV(Swedish Meteorological and Hydrological Institute (SMHI)., 2025). Site index (SI) refers to the dominant height of Norway spruce (G) or Scots pine (T) at 100 years of age.

was applied solely to standardize comparisons among species and does not represent an experimental spacing design. At each site, three poplar plots were established, all with identical layout. Within these plots, wood ash was applied at a rate of 3 Mg ha^{-1} (0,3 kg m$^{2-1}$) to 25 plants by mixing it into the upper 30 cm of soil within a 1 × 1 m area centered on each plant prior to planting (hereafter referred to as Poplar AT), while 10 plants per plot (in total 30 plants, arranged in two rows of five per plot) were left untreated (from now on referred as Poplar UT). At the experimental sites, mechanical soil preparation was performed in rows using an excavator and the plants were manually planted. All experimental sites were fenced to deter browsing. Mean annual temperature and precipitation during the three-year experimental period were obtained from gridded climate data (PTHBV) (Swedish Meteorological and Hydrological Institute (SMHI)., 2025) for each experimental site (Table 1).

2.2. *Plant material and wood ash*

The plant material used for planting was the best genetic material available at the time of planting for all species. Aspens clones number 14, 34, 45, 47, 51 and 76 were selected as the best growing genotypes from the Swedish Aspen (SwAsp) collection (Luquez et al., 2008), hybrid aspen clones SK884012 and SK884015 were purchased at a local plant nursery (Sydplantor, Tingsryd, Sweden, Birch (Ekebo 5), Norway spruce (Elite35 +) and Scots pine (Gottardberg särplock), containerized seedling were purchased at a local seedling nursery (Södraodlarna falkenberg, Sweden). All aspen, birch, spruce, and pine plants were two-year-old containerized stock grown in 500 ml containers. Poplar plants were produced via dormant cuttings collected in February, stored at 4°C, and potted in April into 250 ml containers filled with 83% peat, 5% clay, 7% gravel, 5% hydrograins. Poplar cuttings were grown under field conditions to reach ~40 cm in height and ~4 mm in root collar diameter.

Prior to planting, all the cuttings were stored at + 2°C. At the time of planting, in spring 2020, the height of plants was approximately 40 cm for hybrid aspen and aspen, 50 cm for birch, 40 cm for poplar, 30 cm for Scots pine and 35 cm for Norway spruce. All plants were containerized.

The wood ash applied to planting positions on poplar plots consisted of a mixture of 95% bottom ash and 5% fly ash, reflecting the typical composition of wood ash residues produced by biomass combustion in combined heat and power plants. Bottom ash refers to the coarse fraction collected at the base of the combustion chamber, whereas fly ash is the finer fraction captured from flue gases by particulate filters. The low proportion of fly ash was included to improve the homogeneity and nutrient availability of the ash while minimizing the concentration of potentially harmful trace metals. The ash application rate was 3 Mg ha^{-1} (dry matter basis), corresponding to common operational doses used in forest soil amendment practices in Scandinavia. Ash was mixed into the upper 0–30 cm of soil within a 1 × 1 m area around each treated poplar planting position prior to planting. Ash samples were analyzed for elemental composition using inductively coupled plasma–sector field mass spectrometry (ICP-SFMS) at ALS Scandinavia AB (Luleå, Sweden). Sample digestion followed the S-PS49-FU protocol, with subsequent analysis conducted in accordance with SS-EN ISO 17294–2:2023 and US EPA Method 200.8:1994 (Table S1).

2.3. *Growth measurements, soil analyses and sampling of competing vegetation*

Survival, stem height, and root collar diameter of all plants were measured at planting and re-measured annually at the end of each growing season (November) during the three years following establishment. At each site, soil sampling was conducted at the time of planting. Within each plot, the area was divided into two equal sections and subsamples were taken systematically at the centre of the sections to capture spatial variability. Two subsamples per plot were collected from the 0–30 cm mineral soil profile and combined into a composite plot sample. All plot samples were subsequently pooled into a single site-level composite sample for chemical analysis. Soil samples were analysed at Eurofins Agro Testing Sweden AB (Kristianstad, Sweden) using the ammonium lactate–acetic acid (AL) extraction method (SS 028310:1995–12) and inductively coupled plasma optical emission spectrometry (ISO 11885:2009–09). At all experimental sites, six vegetation samples (one per plot) were collected from a standardized 0.5 × 0.5 m area located at the same relative position within each plot and site, at the centre of the plot. Samples included all above-ground competing vegetation within the frame, including grasses, herbaceous species, shrubs, and naturally regenerated woody plants. Vegetation was dried and weighed to quantify total competitive biomass experienced by the experimental plants (Table 2). Although vegetation height and percent cover were not recorded, competition biomass was highest at the most fertile sites, where ground vegetation coverage was close to complete.

2.4. Statistical analysis

All analyses were implemented in R version 4.5.0 (R Core Team, R, 2025) and conducted in R Studio version 2025.05.1 + 513 and all the plots were produced using the package ggplot2 (Wickham, 2016).

Survival (binary response) was analysed using generalized linear mixed-effects models (GLMMs) with a binomial distribution and logit link function, implemented in the glmmTMB package (Brooks et al., 2017). Survival was recorded annually during the first three growing seasons after planting. Fixed effects included site type (forest land vs. forested arable land), species, year since planting, and their interactions. To account for the hierarchical experimental design and repeated survival measurements of individual plants across years, random intercepts were included for site, plot nested within site, planting row nested within plot (1 | site/PlotID/RowID). Because survival was assessed repeatedly on the same individuals over three years, experiment plant identity (PlantUID) was included as an additional random intercept to account for repeated measurements. To test annual growth rates, we employed a zero-inflated Gamma (ZI-Gamma) generalized linear model using the glmmTMB package (Brooks et al., 2017) due to excess of zeros (16% of the data). The response variable was modelled as a function of site type, species, and year, including their interactions. To account for the hierarchical experimental design and repeated measurements, random intercepts were included for site, plot nested within site, and planting row nested within plot. In addition, plant identity was included as a random intercept to account for repeated annual measurements on the same individuals. The Gamma distribution with a log link was specified for the conditional component, while the zero-inflation component used a constant intercept (ziformula = ~1), assuming homogeneous probability of excess zeros. Final tree height was analysed using linear mixed-effects models (LMMs) using the package lme4 (Bates et al., 2015). Fixed effects included site type, species, and their interaction. Random intercepts were specified for site, plot nested within site, and planting row nested within plot. Model selection and inference were based on Type III Wald chi-square tests using the Anova() function from the car package (Fox and Weisberg, 2018). Post-hoc comparisons between species and between years were done with Tukey's HSD (via the emmeans package (Lenth, 2023), with statistical significance set at $p \leq 0.05$. Model assumptions were evaluated using residual diagnostics. For generalized linear mixed-effects models, simulation-based residual diagnostics were performed to assess dispersion and residual patterns using the DHARMa package (Hartig, 2022), while for linear mixed-effects models, residual and Q–Q plots were inspected to verify normality and homoscedasticity.

To assess overall establishment success of different tree species at the two site types (For/ArFor), a Principal Component Analysis (PCA) was performed using height growth (gh1, gh2 and gh3) and root collar diameter growth (gd1, gd2 and gd3) across three years and survival data in the third year (s3) using the base stat package. PCA was performed on plot-level survival and growth variables expressed in their original units to retain absolute differences in early establishment performance; species-wise standardization was not applied because it would shift interpretation to relative within-species variation. The scores of the first principal component (PC1) were then analysed using a LMM from the package lme4 (Bates et al., 2015) with PC1 as the response variable and site type, species, and their interactions as fixed effects. Site included as a random effect to account for spatial clustering among plots. The models' analyses of variance (ANOVA) estimated marginal means and contrasts are available in separate supplementary tables (S2-S16).

3. Results

3.1. Tree survival differs between species and between years

In For, survival rates were consistent across all species, averaging 90% ± 3% by year 3. Poplar UT was one exception, where plant survival decreased after the second growing period, reaching 60% after three years. In contrast, there was a substantial decrease in survival at ArFor over time. By the year 3, Norway spruce survival was 30% ± 7%, while Scots pine survival dropped to 55% ± 8%. Poplar UT exhibited poor survival also in ArFor (year 3: 60% ± 8%). Poplar treated with wood ash (Poplar AT) had high survival in ArFor, reaching 80% ± 7% by year 3 (Fig. 2, Table S3) which is similar to birch and aspen survival after three years.

3.2. Site type influences species height distribution

Mean height comparisons revealed that hybrid aspen, birch, and Scots pine exhibited greater growth on forest (For) sites than on forested former arable (ArFor) sites (Fig. 3A). In contrast, untreated poplar (Poplar UT) showed the opposite pattern, with taller plants on ArFor sites. For aspen, Poplar AT, and Norway spruce, mean heights did not significantly differ between the two site types (Fig. 3A, Table S7).

Overall, height variability appeared high on forest land (For) sites for most species, as illustrated by broader height distributions (Fig. 3B). In particular, hybrid aspen showed a wider range of individual heights at For sites compared to ArFor, indicating greater within-site variability under forest conditions. Similar patterns were observed for birch,

Table 2

Analysis of soil properties and elemental content. Mean values are presented for soil chemical parameters, including pH, total nitrogen (N), plant-available phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), copper (Cu), iron (Fe), and zinc (Zn), along with cation exchange capacity (CEC), base saturation (BS), and dry weight of vegetation samples (Veg), measured at forested arable land (ArFor) and forest land (For) sites.

Site	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 (%)	Veg (g)
For1	4.1	9.7	0.69	1.2	5.6	1.1	15	0.4	950	0.7	12.5	3.2	68.6
For2	4.3	17.6	1.9	2.4	3.7	0.92	3.2	0.2	520	0.6	14.9	2.2	53.3
For3	5.0	3.9	0.83	1.2	2.9	0.5	1.3	0.2	320	0.2	11.6	1.9	50.3
For4	4.4	26.5	0.47	1	< 2.5	0.89	1.5	0.2	70	0.2	6.9	3.3	53.8
ArFor1	5.2	5.8	1.7	1.7	4	0.63	7.9	0.3	77	0.6	11.9	2.5	143.5
ArFor2	4.7	46.5	1.4	1.7	11	0.88	17	0.2	96	2.5	11.8	5.7	170.9
ArFor3	5.4	9.8	4.9	2.2	29	1.9	9.2	0.3	160	5.7	16.2	10.0	182.1

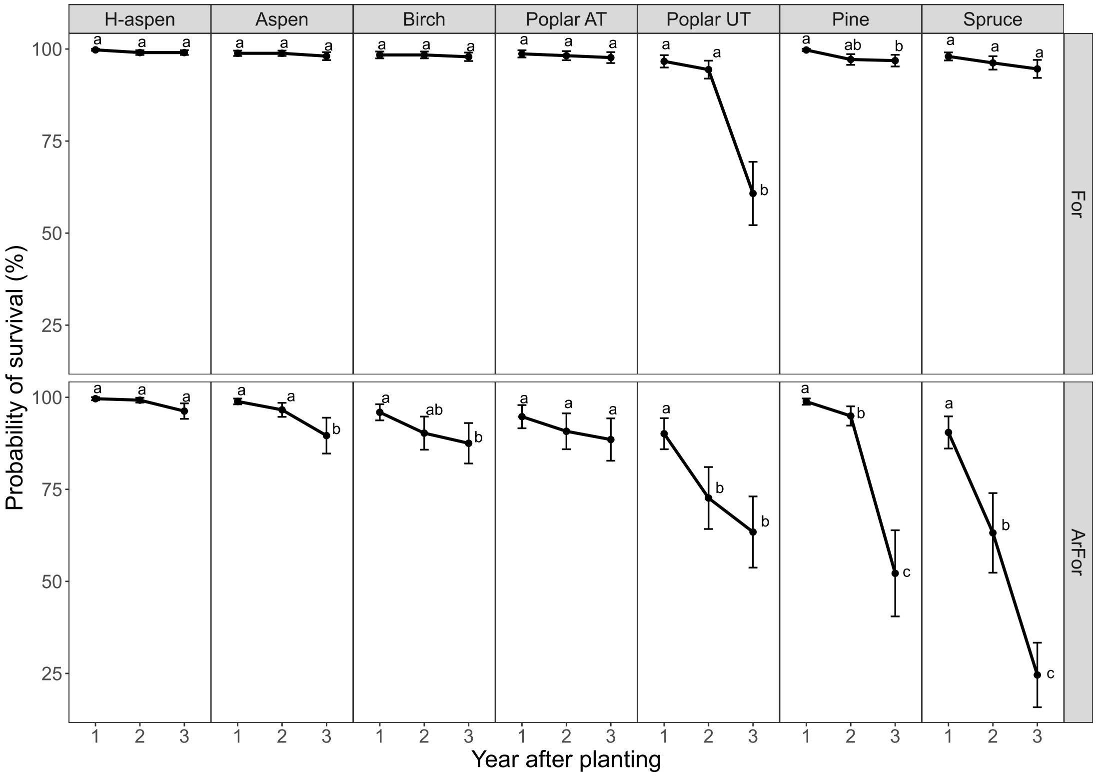

Fig. 2. Plant survival probability (estimated marginal means ± standard error) of six tree species (hybrid aspen, European aspen, silver birch, ash-treated poplar [Poplar AT], untreated poplar [Poplar UT], Scots pine, and Norway spruce) in forest land (For) and forested arable land (ArFor) over the three-year establishment period. Each panel represents a single species, with survival plotted against year after planting. Error bars indicate standard errors, and different letters denote statistically significant differences ($p < 0.05$) among years within the same species and site type.

whereas other species exhibited more uniform height distributions across site types. These patterns are presented descriptively and reflect general variability within site types rather than statistically tested differences among individual sites.

When analyzing the 10 best performing trees per species per site (representing individuals with the highest early growth) the observed trends became more pronounced (Fig. 3C–D). On For sites, hybrid aspen, birch, Scots pine, and Norway spruce all showed significantly greater mean heights compared to their counterparts on ArFor sites (Fig. 3C). Conversely, Poplar UT continued to perform better on ArFor sites, while aspen and Poplar AT showed no significant differences between the two site types. Overall, on For sites, hybrid aspen attained the greatest mean height, whereas on ArFor sites, poplar AT exhibited the tallest growth. At the individual site level, height differences among the top-performing trees highlighted more localized site effects (Fig. 3D). For most species (hybrid aspen, aspen, birch, Poplar AT, Scots pine, and Norway spruce) the highest growth was recorded on For1 and For2. Among ArFor sites, ArFor2 displayed better growth for hybrid aspen, aspen, birch, and Scots pine, although differences were less pronounced than those observed among For sites. Poplar AT, in contrast, showed no consistent growth trend across ArFor sites. The analysis of the tallest individuals per plot is intended to evaluate early dominance development rather than stand productivity. In fast-growing broadleaved plantations, silvicultural decisions such as crop-tree selection and pre-commercial thinning are based on dominant individuals. Examining the height distribution among top performers therefore provides information on whether site conditions limit the development of future crop trees and whether dominant individuals develop uniformly or diverge early, indicating potential stratification within the stand

3.3. *Species-specific annual growth rates are influenced by site type*

Annual height increment differed significantly between site types for several species, and these differences varied across years (Fig. 4; Tables S12–S13).

Hybrid aspen exhibited consistently greater annual height growth on forest land (For) compared to forested arable land (ArFor), 51 vs 37 cm in year one, 107 vs 38 cm in year two, and 138 vs 54 cm in year three. A similar pattern was observed for birch, with significantly higher growth on For sites in years two and three (71 vs 30 cm and 77 vs 27 cm, respectively), while differences in year one were not significant. Scots pine and Norway spruce showed no significant difference between site types in the first two years, but growth was significantly greater on For sites in year three (pine 44 vs 18 cm; spruce 18 vs 10 cm).

For European aspen, annual height increment did not differ significantly between site types in any year (e.g. year three 48 vs 40 cm). Wood ash–treated poplar (Poplar AT) also showed no significant differences between For and ArFor across all three years (e.g. year three 66 vs 79 cm). In contrast, untreated poplar (Poplar UT) exhibited significantly higher growth on ArFor sites in all three years (year one 32 vs 9 cm; year two 44 vs 26 cm; year three 60 vs 22 cm).

3.4. *Overall establishment success*

The first principal component (PC1) summarized variation in early establishment, combining third-year survival probability with height and root collar diameter growth., and is therefore interpreted here as an operational index of early establishment success rather than a comprehensive measure of long-term performance.

The PCA analysis (Fig. 5A) of species growth and survival showed that the first component (PC1) explained over 72% of the data variability, while the second component (PC2) accounted for 12.7%

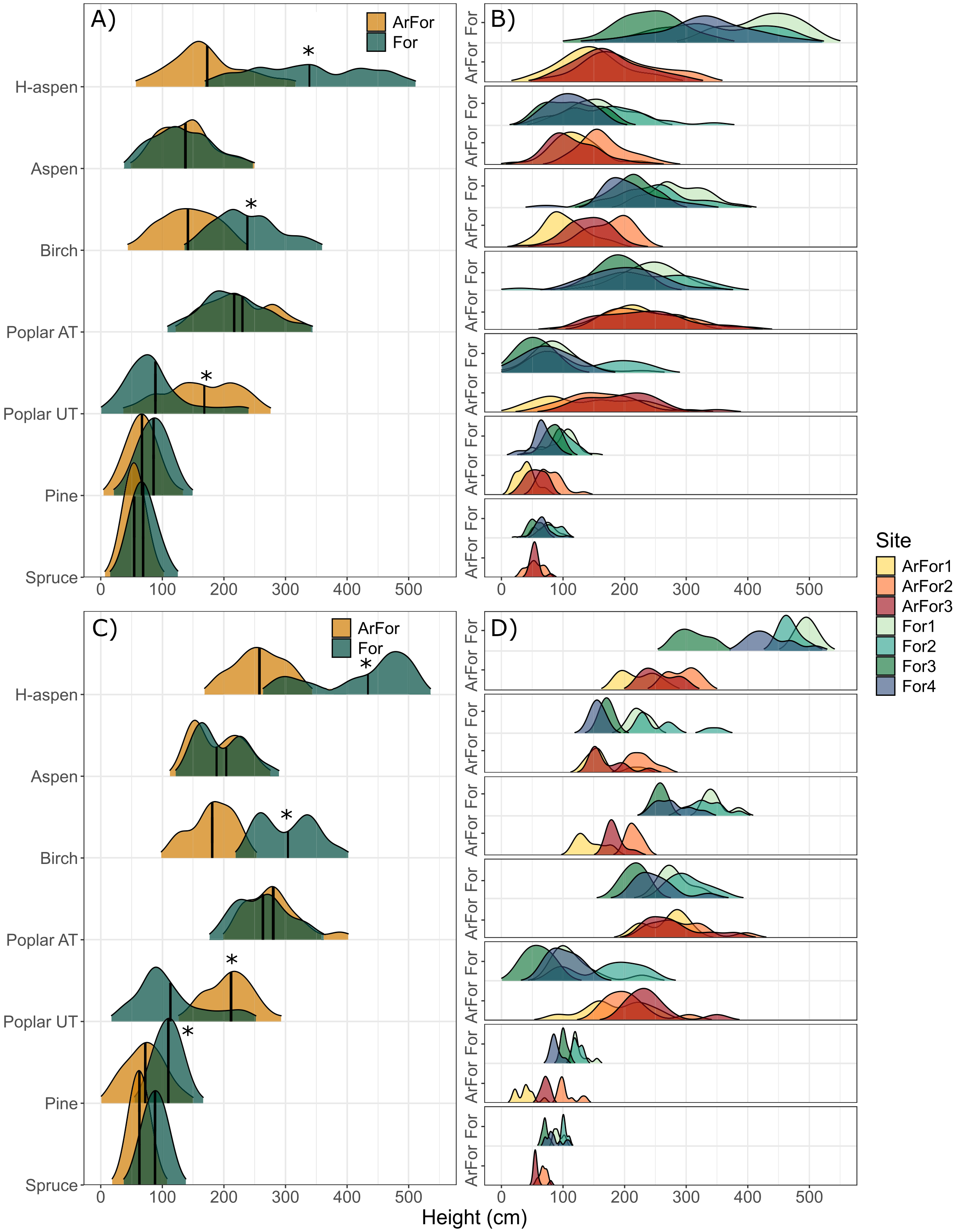

Fig. 3. Density plots showing height (cm) distributions at the third year for hybrid aspen, aspen, birch, poplar ash-treated (poplar AT), poplar untreated (poplar UT), Scots pine, Norway spruce at ArFor (orange) and For (green) after three growing seasons. Vertical lines indicate mean heights, and the spread of each density curve reflects variability within each category. **A)** plant height distribution of all plants across sites. **B)** plant height distribution for the individual experimental sites. **C-D)** shows height density plots of the top 10 best performing plants per species per site (i.e. 200 trees per ha) with (**C**) showing across sites and (**D**) for each individual experimental site. Asterisks denote statistically significant differences ($p < 0.05$) between site types within each tree species.

(Fig. 5A). All of the included variables exhibited positive loadings for PC1, making PC1 an index for “establishment success. Variables with high PC1 loadings (e.g., gh1–3, gd1–3) accounted for most of the variance, consistent with greater variability and stronger correlations in growth metrics compared to survival. The survival variable (s3) displayed a shorter arrow, reflecting weaker loadings on PC1, likely due to lower variance or weaker associations with other variables (Fig. 5A). Growth metrics for height (gh1–3) and diameter (gd1–3) across three years display distinct loading patterns. Early-year metrics (gh1, gd1) show positive loadings on PC1 and positive loadings on PC2, aligning

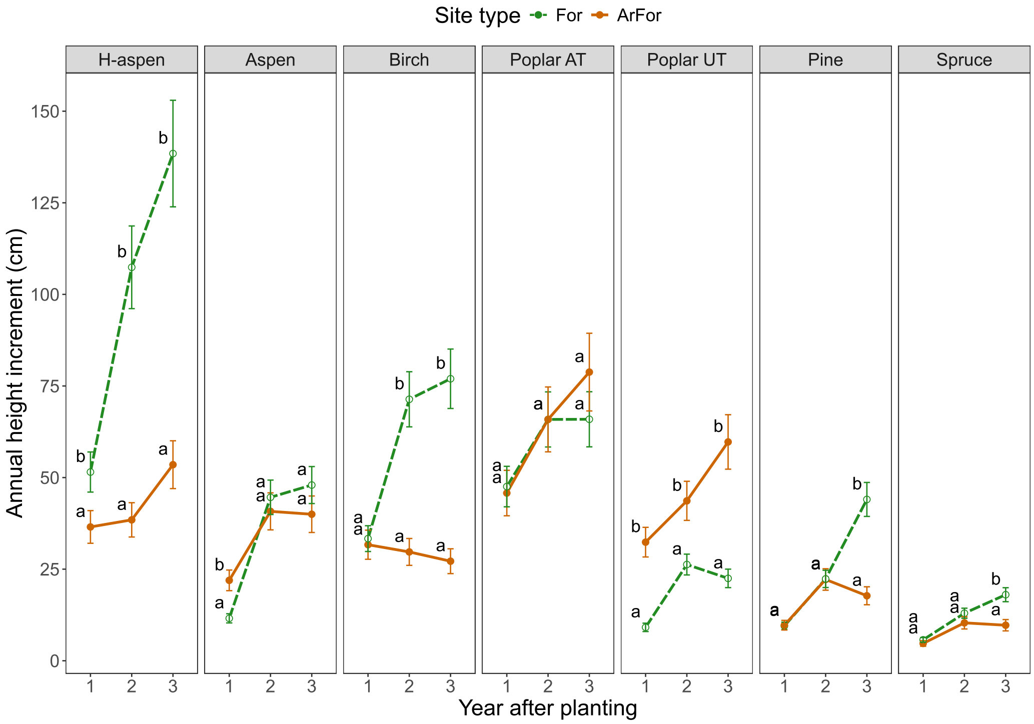

Fig. 4. Annual height increment (cm) of six tree species (hybrid aspen, European aspen, silver birch, ash-treated poplar [Poplar AT], untreated poplar [Poplar UT], Scots pine, and Norway spruce) over the first three years after planting in Forest land (For) and Forested arable land (ArFor). Points represent estimated marginal means with standard errors derived from mixed-effects models, and lines connect yearly means within each site type. Panels correspond to individual species. Letters indicate statistically significant differences between site types within the same species and year ($p < 0.05$). Colors denote site type, with green representing Forest land and orange representing Forested arable land.

more with ArFor sites. In contrast, later-year metrics (gh3, gd3) and survival rate at year three (s3) are negatively loaded on PC2, closely associated with For sites (Fig. 5A). This suggests that although fast initial growth may occur in both site types, sustained growth and higher survival rates over time are primarily associated with For sites. The negative PC2 loadings of early metrics indicate that factors influencing initial growth may differ from those promoting long-term growth and survival, which are more prevalent in For sites. PC2 is interpreted descriptively and is not used for formal hypothesis testing in this study.

The violin plots display PC1 scores derived from Principal Component Analysis (PCA), representing an index of overall establishment success. Among the species, hybrid aspen, birch, aspen, Scots pine, and Norway spruce exhibited significantly higher PC1 scores on forest (For) sites compared to forested arable (ArFor) sites, indicating more successful establishment under forest site conditions. In contrast, poplars UT and European aspen showed no significant differences in PC1 scores between the two site types, while poplar UT showed significant higher PC1 scores in ArFor.

At the For sites, hybrid aspen had the highest PC1 score (~5.3), followed by birch (~2.8) and poplar AT (~2.5), suggesting particularly favourable establishment conditions for these species (Fig. 5B, table S15). On ArFor sites, poplar AT displayed a PC1 score of approximately 1.6, the highest among all species on this site type. In contrast, hybrid aspen exhibited a markedly lower PC1 value (0.8), while birch and aspen had negative PC1 scores (–0.3), indicating reduced establishment success on ArFor sites (Fig. 5B, table S15). These results highlight a strong species-by-site interaction, with certain species (e.g., hybrid aspen and birch) performing better on forest land, while others (poplar AT and aspen) maintain relatively stable establishment success across both site types.

4. Discussion

Our findings indicate that multiple species can contribute to forest diversification, but reforestation success is strongly shaped by the interaction between species traits and site conditions. Hybrid aspen, birch, European aspen (also referred as aspen), and wood ash–treated poplar all showed consistently high survival across the three-year monitoring period, whereas survival was lowest for Norway spruce and Scots pine on forested arable sites (Fig. 2). These differences likely reflect variation in competitive ability during establishment. Pioneer species such as birch, aspen, and poplar are generally sensitive to competition (Whitmore, 1989), highlighting the importance of effective vegetation management (Bilodeau-Gauthier et al., 2011; Böhlenius and Övergaard, 2015; Desrochers and Sigouin, 2014; McCarthy et al., 2011). However, when planted, they often offset this sensitivity through rapid early growth, enabling them to outcompete surrounding vegetation for light (Dalling and Hubbell, 2002; Grossnickle and MacDonald, 2017). Similar patterns have also been documented for Scots pine and Norway spruce establishment (Nilsson, 2020; Sikström et al., 2020). In our study, competing vegetation was more abundant on forested arable land (Table 2), likely due to higher nutrient availability and a persistent seed bank (Grubb, 1977; Jylhä and Hytönen, 2006). This likely constrained Norway spruce and Scots pine establishment, given their comparatively slower early growth, whereas hybrid aspen, birch, and poplar could partially escape competition through rapid height development. Indeed, Jylhä and Hytönen (2006) reported that seedling survival and growth are significantly reduced under dense ground vegetation, conditions that were observed at our ArFor sites. In contrast, when soil preparation effectively suppressed vegetation on forest sites, survival exceeded 80% across all species (Fig. 2). Taken together, these patterns indicate that, while long-term climate resilience depends on physiological and ecological traits that are not directly assessed here, successful early establishment represents a necessary prerequisite for regeneration under

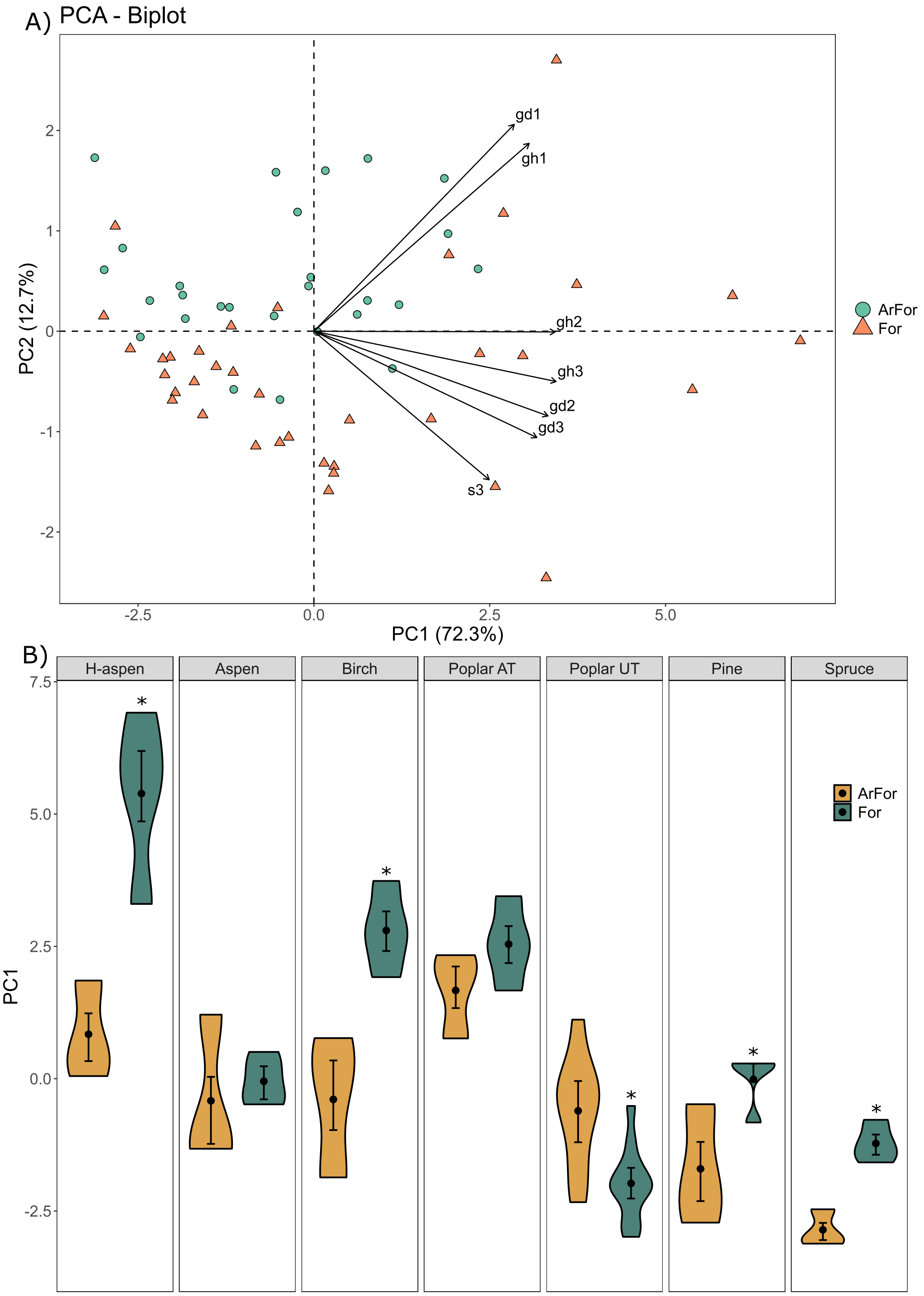

Fig. 5. A) PCA biplot showing the relationship between tree species (hybrid aspen, European aspen, silver birch, ash-treated poplar [Poplar AT], untreated poplar [Poplar UT], Scots pine, and Norway spruce) growth traits (height and diameter measurements) and survival rates across study sites. Variable loadings are represented by arrows,(with shorter arrow representing weaker loadings in the respective Principal Component), with growth metrics (gh1–3, gd1–3, respectively height and diameter growth year 1–3) and survival rate at the third year (s3) shown relative to the principal components. Data points represent individual site observations, with colors distinguishing between site types. **B)** Violin graph showing PC1 scores from principal component analysis for six tree species (hybrid aspen, aspen, birch, poplar AT, poplar UT, Scots pine, Norway 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.

changing environmental conditions.

Our experiment revealed substantial variation in height growth among tree species and between site types (Figs. 3 and 4). In general, trees exhibited better growth on forest land (For) compared to forested arable land (ArFor). Two sites, For1 and For2, stood out for their consistently high growth across most species (Fig. 2). Soil analyses indicated (Table 2) that these sites had high cation exchange capacity (CEC) and base saturation (BS), along with comparatively low ground vegetation biomass. Both sites are located in regions with sedimentary bedrock (sandstone, shale clay, and alum shale), which likely contributes to enhanced soil fertility and supports higher tree growth. These observations suggest that site-specific factors, including geology and thus soil nutrient status, strongly influence early growth performance. Soil chemistry and competing vegetation variables were not included in the PCA because they were measured at the site level, whereas the ordination was based on individual tree responses. Including such variables would introduce pseudoreplication, as multiple observations would share identical explanatory values. A targeted sampling design with within-plot environmental replication would be required to properly evaluate environmental drivers of establishment performance.

Wood ash–treated poplar (Poplar AT) exhibited high growth at both site types, with mean heights of 223 cm on forested arable land (ArFor) and 207 cm on forest land (For), although this difference was not statistically significant. In contrast, untreated poplar (Poplar UT) showed significantly greater height growth on forested arable land (mean ≈153 cm) than on forest land (mean ≈80 cm), despite low survival rates at both site types (≈60–63% by year three), emphasizing the importance of ash treatment for successful establishment. The inferior performance of untreated poplar is likely linked to the low soil pH at all sites (4.1–5.2), which falls below the optimal range for poplar growth. This is consistent with previous studies reporting that poplars generally require more neutral to slightly alkaline soils for optimal growth (Bergstedt, 1981; Bona et al., 2008; Thomaes et al., 2012) and that application of wood ash on acidic soils increases growth (Arseneau et al., 2021; Bona et al., 2008; Muraro et al., 2025) A recent Scandinavian study by Crut (2025) has shown that poplars can achieve high productivity on forested arable land sites, with yields reaching approximately 16 m^3 ha^{-1} yr^{-1} over a 15-year rotation period. These yields were approximately 30% lower than those obtained on arable land, highlighting a trade-off between productivity and site type that should be considered when evaluating poplar deployment on forested arable land. This suggests that, with appropriate site management (e.g. ash treatment), poplar plantations could represent a viable reforestation option on fertile forested arable land sites, although production expectations should be adjusted relative to arable land systems.

In line with earlier studies, our results confirm that hybrid aspen has strong establishment potential, combining rapid early height growth with high survival (Figs. 2,3 and 4). While previous work has largely highlighted its productivity on arable land (Fahlvik et al., 2019; Johansson, 2013; Rytter and Stener, 2014), evidence from forest and forested arable sites remains scarce. Our findings suggest that, under suitable site conditions, hybrid aspen can establish successfully beyond traditional arable environments, thereby broadening the range of sites where it could be used. This makes hybrid aspen a promising option for diversifying forest stands and enhancing resilience, especially given its pioneer traits and ability to compete effectively with surrounding vegetation. Although long-term productivity data are still needed, strong early performance is an important prerequisite for future yield and stand stability (Rytter and Lutter, 2020).

In our experiment, silver birch demonstrated strong potential as a broadleaf species for diversification at forest sites, with high survival rates (∼80%) significantly higher growth on forest land (mean ∼75 cm by year 3) than on forested arable land (∼30 cm), reflecting better establishment success under less competitive and more nutrient-limited conditions (Fig. 5). This pattern aligns with the adaptability of birch to nutrient-poor, acidic soils commonly found in Nordic forests (Hynynen et al., 2010). Although growth slowed between years two and three (Fig. 3), birch early vigor and survival underscore its value as a native option for species diversification strategies, supporting biodiversity and offering potential for shorter rotations and enhanced structural diversity. During recent years there has been a major improvement in yields of planted birch as a result of implementation of breeding programmes, resulting in MAIs up to 14 m^3 ha^{-1} $year^{-1}$ compared to 6–12.8 m^3 ha^{-1} $year^{-1}$ from previous birch plant material (Liziniewicz et al., 2022).

The aspen plants used in this study, exhibited high site-adaptability, achieving median heights of 150 cm and similar survival levels across forest and forested arable sites. This performance reflects the ecological versatility of European aspen, which occurs across a broad geographic range and thrives on a wide variety of soil types throughout Europe and Asia (Caudullo et al., 2017; Kusbach et al., 2024). Despite its adaptability, aspen has historically been undervalued in commercial forestry (Edenius et al., 2011; Kusbach et al., 2024) and has not been widely considered for large-scale production. However, due to its ecological importance - serving as habitat for a wide range of bryophytes, lichens, insects, and birds - it has maintained an important role in forestry as a key species for promoting biodiversity in forest landscapes (Caudullo et al., 2017; Kouki et al., 2001; Mönkkönen et al., 2014). Studies from the late 1990s estimated aspen production levels at approximately 7.9–13.9 m^3 ha^{-1} yr^{-1} , which are generally lower than those reported for hybrid aspen (Lutter et al., 2017). This aligns with our findings, where aspen showed high survival and site adaptability, but more modest height growth compared to hybrid aspen. Previous studies have further demonstrated that by 5–7 years after planting, hybrid aspen stem volume exceeds that of native aspen by three- to fourfold (Yu et al., 2001), emphasizing the productivity gap between unimproved aspen and its hybrid counterpart. It is important to highlight that most trials, including our study, use unselected aspen material with no prior genetic improvement. The clones used in this study, while the best-known aspen material available from a nationwide collection, originated from up to 5 latitudinal degrees north of the experimental sites and were thus maladapted to the intrinsic photoperiod with resulting consequences for growth. We would predict that considerable growth advantages could be gained by sourcing local aspen provenances to capture home-site advantage. To enable large-scale deployment of aspen, breeding and clonal selection would be necessary. Traits such as drought tolerance and resistance to browsing - currently major limitations for successful establishment of *P. tremula* - could be targeted through vegetative propagation. Such selection has been estimated to improve volume growth by 10–25% within two decades (Jansson et al., 2017; Ruotsalainen, 2014). While conventional breeding in long-lived species like aspen requires breeding cycles of 20–30 years (Grattapaglia, 2017; Lebedev et al., 2020), emerging technologies such as genomic selection and biotechnology offer promising alternatives by accelerating breeding timelines and enabling earlier identification of superior genotypes (Ahmar et al., 2021; Grattapaglia, 2022). Beyond biological considerations, improved native European aspen may also offer advantages in terms of social acceptance, as Swedish forest owners and certification frameworks have historically shown greater acceptance of native species than of hybrid or non-native alternatives (Hemström et al., 2013).

Although the present study did not include mixed-species stands, the strong early establishment of hybrid aspen, birch, and wood ash–treated hybrid poplar highlights traits that could be relevant for future diversification or nurse-crop strategies under appropriate competition control. Birch has long been shown to function as a shelter or nurse species for Norway spruce in Fennoscandia (Frivold and Frank, 2002; Lundqvist et al., 2014; Mård, 1996; Valkonen and Valsta, 2001), benefiting from its relatively open canopy structure and capacity to moderate microclimatic extremes (Navarro-Cano et al., 2019).

While the use of hybrid aspen as a nurse species remains largely unexplored in northern Europe, analogous systems involving trembling aspen and white spruce in North America have demonstrated facilitative effects on spruce establishment and growth (Kabzems et al., 2016; Lieffers et al., 2018; Pitt et al., 2015). Given its high survival and rapid early height growth at forest sites in this study, hybrid aspen may therefore represent a promising nurse-crop candidate under suitable site conditions. European aspen, although exhibiting more modest early height growth than hybrid aspen, showed consistently high survival and broad site adaptability. This suggests that it could also be considered in future mixed-species trials, particularly where ecological compatibility, biodiversity values, and social acceptance are prioritized over rapid canopy closure. Wood ash–treated hybrid poplar (Poplar AT) also exhibited strong early growth on forested arable land, indicating its suitability for establishment on fertile sites. Although hybrid poplar is shade-intolerant, previous studies suggest that it can be integrated into short-rotation systems that precede or facilitate the establishment of shade-tolerant species (Josiah and Kuhn, 2000; Nelson et al., 2012; Stark et al., 2015). However, our results indicate that high competitive pressure on forested arable land remains a major constraint for Norway spruce establishment, and any potential nurse effect would likely depend on concurrent vegetation management. Importantly, successful establishment of hybrid poplar under these conditions required ash treatment, emphasizing that its potential role as a nurse or preparatory species is contingent on appropriate soil amendments and site preparation.

Overall, the results from this study do not demonstrate facilitation in mixed stands but rather identify species with strong early establishment traits that could be considered in future experimental trials explicitly designed to test mixed-species regeneration strategies.

Although hybrid aspen and hybrid poplar are relatively short-lived species, their potential contribution to forest resilience should be considered primarily at the landscape and management-system level rather than in terms of long-term stand persistence. Fast-growing broadleaved species can facilitate rapid establishment and early canopy closure following disturbance or harvest, thereby shortening recovery times and reducing the risk of regeneration failure associated with competition and microsite stress (Berkowitz et al., 1995; Marks and Bormann, 1972). When deployed across forest landscapes, even as monocultures at the stand level, such species increase functional and compositional diversity, which can reduce the likelihood of large-scale synchronous failures driven by pests, drought, or extreme weather events (Mina et al., 2022; Sebald et al., 2021). In addition, shorter rotation lengths increase management flexibility, allowing forest managers to adjust species choice and silvicultural strategies more rapidly in response to changing climatic and economic conditions (Subramanian et al., 2015). In this context, resilience emerges from faster recovery, risk spreading, and adaptive capacity rather than from stand longevity alone.

When considering both survival and growth performance, all planted tree species, except poplars (both AT and UT), generally performed better on forest land than on forested arable land, a pattern consistent with previous studies highlighting the importance of site history and vegetation competition during establishment (Jylhä and Hytönen, 2006; Stener and Westin, 2017). However, the experimental design did not include paired forested arable land sites at all study locations. In particular, the most fertile forest sites (For1 and For2), which exhibited the highest growth across species, lacked corresponding forested arable land counterparts. As a result, site-specific factors such as soil fertility and geological setting may have contributed to the observed differences between land-use types. A fully balanced design with paired forest and forested arable sites at all locations would be required for a more robust separation of land-use effects from site-specific influences.

Poplar AT exhibited comparable growth across both site types; however, their annual height increment peaked earlier (in year two) on forest land, while growth continued to increase until year three on forested arable land. Similar growth responses of poplars on fertile former agricultural sites have been reported and linked to sustained nutrient availability and favourable soil conditions (Christersson, 2008, 2010; Rytter and Lutter, 2020). This pattern suggests that poplars may achieve greater long-term productivity on forested arable sites (Figs. 3 and 4), although longer-term studies are required to confirm this.

Hybrid aspen, birch, Scots pine, and Norway spruce showed superior performance on forest land, whereas poplars and European aspen performed similarly across both environments (Fig. 5). Together, these results align with previous work indicating that native broadleaved species such as birch and aspen, as well as fast-growing hybrid taxa, can establish successfully following final harvests when matched to suitable site conditions (Hynynen et al., 2010; Mc Carthy et al., 2017; Rytter et al., 2013).

However, broader integration of non-native species in Swedish forestry must navigate existing certification schemes. A large share of Swedish forest land - nearly 15 million ha, about 65% of productive forest area - is certified under schemes such as the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC) (Skogsdata, 2025). These frameworks impose limits on the use of non-native species: FSC typically restricts their use to 5% of productive forest land, while PEFC allows up to 20% for large forest owners (FSC, 2020; PEFC, 2023). Despite these restrictions, current plantation areas of hybrid aspen and poplar remain modest - under 10, 000 ha (Mc Carthy, 2016) - suggesting considerable untapped potential within existing certification limits. Moreover, FSC permits the replacement of one non-native species with another, offering further opportunity to expand poplar cultivation. This is especially true in the southernmost part of Sweden (Skåne), where Norway spruce is classified as non-native species. In this context, replacing aging Norway spruce stands on forested arable land with fast-growing species such as poplar could represent a pathway for diversifying future forests.

4.1. Practical implications for diversification using broadleaves in conifer-dominated forest regions in Northern Europe

Our results indicate several promising options for increasing tree species diversification, though important site-specific factors must be considered. On fertile forest sites, represented here by forested arable land, poplars demonstrated a clear advantage over other species in terms of early growth. Soil analysis proved to be a crucial tool for assessing the suitability of poplar planting, with observed soil pH values around 5.0. In this study, wood ash treatments enhanced poplar establishment and early growth, suggesting that forest managers should strongly consider incorporating wood ash into planting protocols as an effective strategy to improve establishment success.

On less fertile forest land, species naturally adapted to nutrient-poor and acidic conditions, such as hybrid aspen and birch, exhibited high establishment success. This early performance likely translates to increased productivity, improved carbon sequestration, and shorter rotations, providing earlier economic returns for forest owners. Conifers remain a viable option for reforestation at these sites, but longer rotation lengths are expected.

It is important to note that our findings are based on observations from the first three years after planting and therefore primarily reflect early establishment and initial growth performance. Long-term studies are needed to assess sustained productivity, full economic performance including establishment costs and end-product values, carbon sequestration, and resilience to climatic extremes across rotation lengths. While genetic improvement was not examined directly in this study, the observed variation in early growth and survival among species highlights the potential importance of selecting well-adapted plant material, particularly for species such as European aspen that currently lack extensive breeding programs. Further gains in productivity and establishment success are therefore likely to depend on improved matching of species and genetic material to site conditions. In addition, the strong early establishment of fast-growing broadleaves such as hybrid aspen, birch, and hybrid poplar suggests that these species warrant further investigation in experimental designs explicitly testing mixed-species regeneration and facilitative interactions under Nordic conditions.

CRediT authorship contribution statement

Henrik Böhlenius: Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Luca Muraro:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Robinson Kathryn Megan:** Writing – review & editing, Methodology. **Mateusz Liziniewicz:** Writing – review & editing, Methodology.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123642.

Data availability

Data will be made available on request.

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