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Growth, spring phenology and stem quality of four broadleaved species assessed in provenance trials in the Netherlands - Implications for seed sourcing

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Local seed sourcing from autochthonous tree populations is widely practiced for biodiversity conservation, as they are presumed to be adapted to local environmental conditions. Yet, autochthonous seed sources are not registered in the Netherlands for timber production, as these stands often exhibit poor stem quality due to their coppice history. Here, we study whether the performance of registered local seed sources from autochthonous origin (category "Source identified") differs from local seed sources selected or improved for forestry purposes. We analyzed survival, growth, spring phenology, and stem form in four single-site provenance trials. In total, seeds from 74 provenances of four broadleaved species (*Alnus glutinosa*, *Betula pubescens*, *Fagus sylvatica*, and *Quercus robur*) were collected and planted in four provenance trials between 2008 and 2010. Provenance effects were consistently significant for budburst, whereas the effects on survival, growth, and stem form varied by species. *Betula pubescens* showed a 169% height difference between provenances at age 12, with several autochthonous provenances outperforming seed orchard material. In the other species, several autochthonous provenances performed equally well in terms of growth compared to seed sources in the "Tested" category. Differences in budburst timing were particularly evident in *Fagus sylvatica* and *Quercus robur.* In these trials, the autochthonous provenances were among the latest in flushing compared to the other local seed sources. Principal component analysis revealed strong correlations between growth and budburst, especially in *Fagus sylvatica* and *Quercus robur*, where earlier flushing was linked to greater height. This highlights potential trade-offs in selecting for both growth and late budburst. Overall, the study demonstrated that even within the ecologically uniform Dutch environment, genetic differences are present between local seed sources. We conclude that autochthonous provenances, despite exhibiting inferior phenotypic characteristics *in situ* due to past intensive silvicultural practice, can possess good growth and form characteristics, which makes them suitable for seed collection for both ecological and production purposes.

Keywords: Provenance Trials, Growth, Stem Form, Spring Leaf Phenology, *Alnus glutinosa*, *Betula pubescens*, *Fagus sylvatica*, *Quercus robur*

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Introduction

The selection of seed sources used for producing forest reproductive material is of major concern for the vitality, productivity, and persistence of forests (Jalonen et al. 2018, Vitt et al. 2022, Leites & Benito Garzón 2023). To mitigate climate change and enhance forest resilience, there is a growing demand for seed sources for high-quality forest reproductive material (FRM) that is well-adapted and genetically resilient (FAO 2025). However, seed sources can differ in their performance for multiple traits, including productivity characteristics such as survival and yield, as well as in their adaptability to environmental challenges, as shown by decades of provenance research (Aitken 2004, Koskela et al. 2014). Even within small geographic ranges, provenances may significantly differ in phenotypic traits (Jensen 2000, Müller & Finkeldey 2016, Wunderlich et al. 2017, Lobo et al. 2018, Buras et al. 2020). For example, Müller & Finkeldey (2016) studied the performance of *Fagus sylvatica* seedlings from six provenances growing along a temperature and precipitation gradient in Northern Germany in a common garden experiment. Despite the small distances between seed origins, they found significant differences in height and mortality. However, precipitation at the original provenance location had no influence on the performance of the provenances. Similarly, Wunderlich et al. (2017) found clear differences in growth between locally sourced provenances from the federal state of Baden-Württemberg in trials of *Quercus robur* and *Picea abies* in Germany. In their study a relationship between the altitude of origin and height growth was found mainly in *Picea abies*. Buras et al. (2020) demonstrated soil-type-specific growth patterns in locally sourced provenances of *Quercus robur* in the Neth-

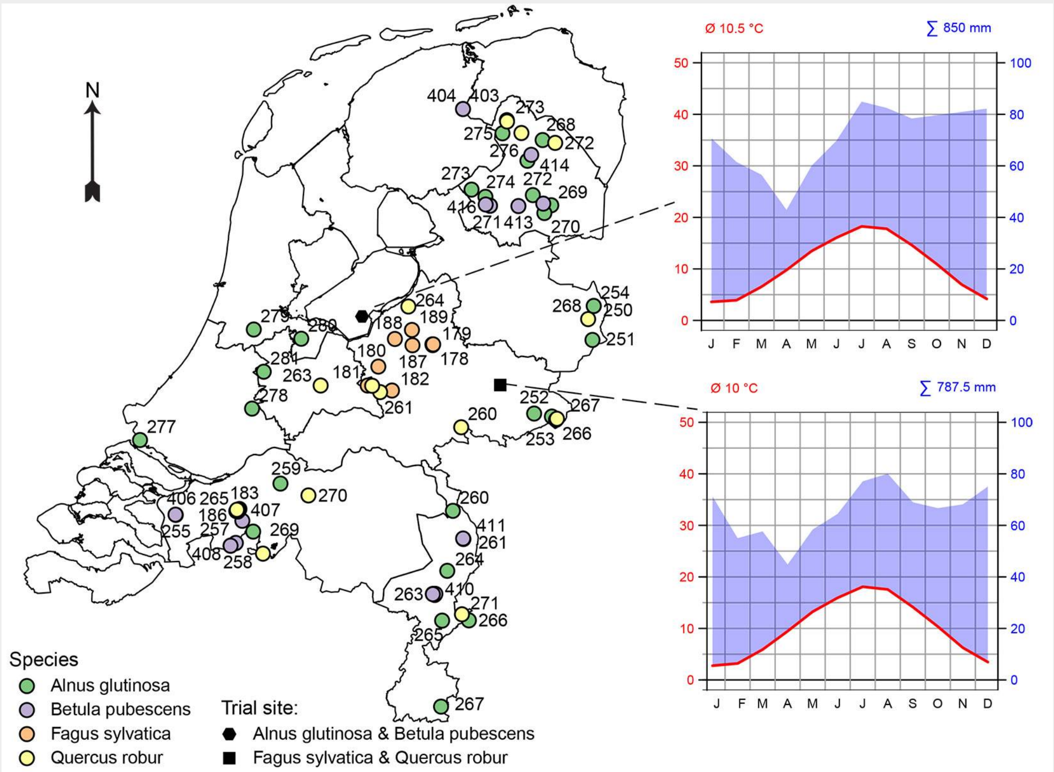


Fig. 1 - Provenances included in the provenance trials and locations of the trials in the Netherlands, along with their Walter-Lieth climate diagrams (1990-2019).

erlands, highlighting the importance of soil conditions (*e.g.*, clay *versus* sand) in evaluating growth performance. This indicates that not only broad geographic trends, but also small-scale variations in microclimate, soil conditions, or site history can drive local adaptation. These findings highlight the importance of carefully selecting provenance in forestry practices, even when sourcing seeds locally, to ensure the optimal growth and adaptability of forest stands. Local seed sources can be autochthonous, meaning that they are populations that have spontaneously colonized the area after the last glaciation or have been artificially propagated from material collected from the same population or within autochthonous populations in close proximity. These trees have grown and reproduced in a particular place for thousands of years (Council of the European Union 2000). These populations are presumed to be characterized primarily by their adaptation to local environmental conditions and their unique genetic makeup (Kleinschmit et al. 2004). In the Netherlands, not all local seed sources are of autochthonous origin, and therefore, a distinction is made between autochthonous and other local seed sources of non-autochthonous or unknown origin. Forest reproductive material in the Netherlands is regulated under the Seeds and Planting Materials Act (Overheid.nl 2005), which enforces Council Directive 1999/105/EC on the marketing of forest reproductive material across the EU. In the national register of approved basic material (Anonymous 2025), the category "Source identified" is reserved exclusively for local material with autochthonous origin. These autochthonous planting materials are primarily used for ecological purposes, including nature restoration or landscaping (*e.g.*, hedge rows) to support biodiversity conservation. While research on the impact of the origin of seed sources on interactions with associated biodiversity remains limited (Broadhurst et al. 2008), there is some evidence that suggests that local seed sources play a key role in supporting pollinators and pathogen resistance (Jones et al. 2001, Cunningham et al. 2005, Bucharova et al. 2016). For instance, non-local provenances of *Crataegus monogyna* produced buds up to five weeks earlier than local ones, potentially disrupting the plant-*Lepidoptera*-bird food chain. Local provenances also exhibited the mildest mildew symptoms (Jones et al. 2001). Given the increasing demand for FRM in response to the new Dutch Forest strategy (LNV 2020) – in which large-scale forest restoration plantings are foreseen –, selecting autochthonous planting material that simultaneously supports biodiversity conservation, landscape restoration, and high-quality wood production would be advantageous in the context of the Netherlands' multifunctional forest management approach.

Autochthonous populations in the Netherlands are relatively scarce (Maes et al. 2021). This scarcity is primarily due to historical deforestation and intensive forest exploitation, large-scale land consolidation during the Middle Ages (Maes 2006). By the beginning of the 19th century, the area of forest had been drastically reduced to only 4% of the total land area (Dirkx 1998). This was driven by various factors, including the need for wood for construction, shipbuilding, fuel, metal smelting, oak bark for tanneries, as well as land conversion for agriculture and other uses (Buis 1985). From the 1950s onwards, large-scale land consolidation and widespread use of foreign planting material in reforestation efforts further fragmented and declined autochthonous populations (Maes 2006). Evidence for autochthonous status relies on a combination of historical information (*e.g.*, ancient woodland indicators from old topographic maps), ecological site characteristics, and tree characteristics that indicate a high naturalness. For *Quercus petraea* and *Quercus robur*, chloroplast DNA haplotype analysis has also been employed to infer autochthony, as it allows a retrospective analysis of the impact of human-mediated seed transfer within a region (Buiteveld & Koelewijn 2006). Although there is an interest in planting autochthonous provenances for production purposes, to date none of these seed stands have met the phenotypic criteria required for classification in the higher "Selected" category. As most autochthonous populations are found in ancient woodlands, defined in the Netherlands as forests that appear on the earliest topographical maps (c. 1850) and have existed continuously for several centuries, they show signs of old historical use, in particular coppicing. Coppice woodland was by far the most important forest type in the Netherlands until the beginning of the last century. With the decline of active coppice management, most coppice woodlands have either been converted to high forest or left unmanaged. In cases where conversion occurred, one shoot per stool was typically retained to form the basis of a new high forest (Buis 1985, Jansen & Kuiper 2001). However, the resulting timber quality was generally poor. The stems of coppice stools may grow straight up, but under the influence of drifting sand, grazing (*e.g.*, by sheep) or sea wind, resprouted shoots often exhibit malformed growth (Ludwig & Maes 2006). Today, the structural characteristics of these ancient woodlands still reflect their origins as former coppice systems, despite having undergone several decades of natural, unmanaged development. Due to the low stem quality of these stands, they are not suitable for registration in the category "Selected" nor for the selection of plus trees within these stands for seed orchard establishment. Because these poor phenotypic characteristics resulting from historical forest management practices, mainly coppicing, provide little information about the underlying genetic potential, this can only be assessed by research in provenance trials. But so far, few autochthonous provenances have been included in provenance trials in the Netherlands.

In this study, we evaluated the performance of registered Dutch local seed sources from four widespread European tree species, namely, *Fagus sylvatica, Quercus robur, Alnus glutinosa*, and *Betula pubescens,* in provenance trials. *Fagus sylvatica* and *Quercus robur* are very common and economically valuable forest tree species that have been extensively studied in earlier provenance trials (Jensen 2000, Von Wuehlisch 2007, Robson et al. 2018). *Alnus glutinosa* and *Betula pubescens* are economically less important species in western Europe and have received little attention in provenance studies (Verwey 1977, Kleinschmit & Otto 1980, Billington & Pelham 1991, Riege & Sigurgeirsson 2018). Both are pioneer species that are valued mainly for their ecological functions and abilities to grow under moist conditions (Beck et al. 2016, Durrant et al. 2016).

We aimed to compare local autochthonous seed sources of category "Source identified" (SI), known to have naturally regenerated and without phenotypic selection, with local planted seed sources in the category "Selected" (S) and in the improved categories "Tested" (T) and "Qualified" (Q) for productivity, stem quality, and budburst. All seed sources were from the Netherlands, which is considered a region of provenance. We were particularly interested in (i) assessing differences between local seed sources in spring leaf phenology, (ii) evaluating the genetic potential of autochthonous seed sources that exhibit poor stem form due to historic management, specifically former coppice, and (iii) identifying provenances that perform well for multiple traits. Ultimately, we provide recommendations for each species on which autochthonous provenances to use in Dutch forestry, taking into account both productivity and ecological objectives.

Material and methods

Plant material and experimental design

In total 74 provenances were selected for testing: 13 for *Fagus sylvatica*, 13 for *Betula pubescens*, 16 for *Quercus robur,* and 32 for *Alnus glutinosa* (Fig. 1, Tab. S1 in Supplementary material). The total number of seed sources tested varied by species, depending on the number of seed stands registered and the availability of seed harvests. All provenances were (formerly) registered seed sources of the Dutch register of approved basic material. These include seed stands of autochthonous origin in the category "Source Identified" and planted seed stands of unknown or non-autochthonous origin in the category "Selected" and "Tested" (Kranenborg et al. 2010). The majority of the "Selected" and "Tested" seed stands of *Quercus robur* and *Fagus sylvatica* are roadside and estate plantations. For *Betula pubescens* also a seedling seed orchard (category "Qualified") was included in the trial. The Netherlands does not distinguish different regions of provenance, so all seed sources in the trials were derived from the same region of provenance (NL). More detailed information about the origin of the provenances and their type of basic material is presented in Tab. S1 (Supplementary material).

The experiment was originally established as a randomised complete block design (RCBD), with three complete replicated blocks. Each block contains all provenances, randomly assigned to plots. Each plot initially consisted of 25 (5 × 5) trees of the same provenance. Each block had exactly as many plots as the number of provenances (32 in *Alnus glutinosa*, 14 in *Betula pubescence*, 13 in *Fagus sylvatica* and 16 in *Quercus robur*). However, due to limitations in plant material availability, for *Quercus robur, Betula pubescens* and *Fagus sylvatica* one or two provenances were represented in only two blocks, resulting in a slightly unbalanced and incomplete block design. The trials of *Alnus glutinosa* and *Betula pubescens* were located in the forest area Horsterwold, in the middle of the Netherlands (52° 20′ 34″ N, 05° 29′ 28″ E) on a clayey soil (Fig. 1). Here, two-year-old seedlings were planted at a spacing of 1.5 × 1.25 m in spring 2008. The trials of *Quercus robur* and *Fagus sylvatica* were established in the eastern part of the Netherlands (52° 04′ 20″ N, 06° 22′ 41″ E and 52° 04′ 03″ N, 06° 22′ 31″ E, respectively) on a sandy soil (Fig. 1). Here, two-year-old *Quercus robur* seedlings and *Fagus sylvatica* three-year-old seedlings were planted at a planting spacing of 1.5 × 1.5 m in spring 2008 and 2010, respectively. No thinning was performed in the trials before the measurements.

Both sites are characterized by a maritime climate with mean temperatures of approximately 10 °C and annual precipitation of 788 mm and 850 mm, respectively (Fig. 1). For each site, climate data from a nearby climate station (De Bilt, Twente, respectively) were downloaded from KNMI. The corresponding Walter-Lieth climate diagrams are depicted in Fig. 1.

Assessments

In all trials, survival, height, diameter at breast height (DBH), budburst, stem straightness, and forking were assessed (Tab. 1). Survival was assessed 11-14 years after planting. Tree height and DBH were measured for every surviving tree 10-12 years after planting (Tab. 1). Budburst was recorded 4 to 8 years after planting for each tree separately in 3 consecutive years following a 5-step scoring protocol: (1) dormant winter bud; (2) buds expanding; (3) budburst, first green is visible; (4) leaves are flushing; and (5) leaves are fully expanded. The assessments were conducted only once a year in the spring. The date of assessment was chosen so that a wide variation in budburst scores occurred among the trees in the trial. In the third year (2016) observations for beech were conducted too late in spring, resulting in a lack of observable variation. Consequently, these data were excluded from further analyses. Stem straightness and forking were assessed 11-14 years after planting. For straightness, a 5-step scale was used: (5) absolutely straight stem; (4) fairly straight (only one direction slightly crooked); (3) slight to moderate bends in different directions; (2) moderate to strong bends; and (1) no straight stem. Also forking was scored on a scale ranging from 5 to 1: (5) no fork; (4) branch with a similar angle; (3) fork(s) only in the upper half of the tree height; (2) fork(s) only in the lower half on the tree height; and (1) forks developed both in upper and in lower half of the tree height.

Statistical analysis

All data analyses were performed with the statistical software R v. 4.2.0 (R Core Team 2024). A significance level of α=0.05 was used for statistical testing. Each species had one trial located at a single site, and therefore the analyses were conducted separately for each species.

Field experiments are often subject to systematic spatial variation, *e.g.*, due to soil gradients, microtopography, or water availability, which are typically not captured by blocking alone. Ignoring these spatial trends may lead to inflated error variance and biased provenance estimates. Instead of a linear model such as ANOVA with block as a factor, R package "SpATS" (Rodríguez-Alvarez et al. 2018) was used to model spatial variation and adjust trait values for spatial noise. The model in SpATS was ran using the PSANOVA algorithm. This is a semi-parametric linear mixed model, which includes provenance as a fixed effect, and smooth spatial surfaces as random effects over the row and column coordinates of the plots. SpATS models both fixed provenance effects and spatial trends simultaneously, and can be summarised as:

Tab. 1 - Summary of measured traits per species and age at measurement.

Trial site	Species	Trait	Age after planting (years)	Year of assessment
Horsterwold	*Alnus glutinosa*	Survival	14	2022
		Height	11	2019
		Diameter	11	2019
		Budburst	5	2013
		Budburst	6	2014
		Budburst	8	2016
		Straightness	14	2022
		Forks	14	2022
	Betula pubescens	Survival	14	2022
		Height	12	2020
		Diameter	12	2020
		Budburst	6	2014
		Budburst	7	2015
		Budburst	8	2016
		Straightness	14	2022
		Forks	14	2022
Zelle	*Quercus robur*	Survival	13	2021
		Height	12	2020
		Diameter	12	2020
		Budburst	6	2014
		Budburst	7	2015
		Budburst	8	2016
		Straightness	13	2021
		Forks	13	2021
	Fagus sylvatica	Survival	11	2021
		Height	10	2020
		Diameter	10	2020
		Budburst	4	2014
		Budburst	5	2015
		Budburst	6	2016
		Straightness	11	2021
		Forks	11	2021

$$y = X\beta + X_s\beta_s + Z_s s + Z_u u + e \qquad (1)$$

where the vector *y* contains the trait values averaged per plot (3 plot means per provenance), *β* is a vector of fixed terms including the intercept and provenance effects, and *X* is the respective design matrix. $X_s\ \beta_s$ represents linear fixed effects for row and column coordinates of each plot. $Z_s\ s$ is the random penalized component modelling the smooth spatial surface. Finally, $Z_u\ u$ is a random component that accounts for discontinuous spatial variation. More details of the model are provided in the original publication (Rodríguez-Alvarez et al. 2018). Best Linear Unbiased Estimates (BLUEs) of the traits were obtained for each provenance, corrected for spatial trends. The SpATS package does not perform an overall test for provenance, therefore the R package ASReml-R (Butler et al. 2023) was used with a similar model as that of SpATS. With ASReml-R, a Wald test of Provenance was conducted. Pairwise comparisons based on *t*-tests were performed with the function *LSD.test* in the R package "Agricolae", using the False Discovery Rate adjustment for multiple testing. Finally, provenances were classified into groups based on pairwise comparisons. For each trait, the input consisted of mean values per plot, computed from individual tree measurements. For height (m) and diameter (cm), directly measured continuous values were averaged per plot. For survival, we used the proportion of surviving trees per plot. For ordinal traits such as budburst, forks, and straightness, individual scores (1-5) were averaged per plot, resulting in continuous values suitable for linear models. These plot averages were used as input for SpATS, along with the corresponding plot coordinates. Pearson's correlation coefficient (r) was applied to provenance mean values to evaluate the consistency of budburst scores for each provenance across different years. A principal component analysis (PCA) was performed, using the R function *prcomp* to describe the tested provenances and associations between the traits. PCA is a dimensionality reduction method that converts many correlated traits into a smaller number of uncorrelated variables called principal components, allowing a summarized view of traits and provenances. As input for PCA, adjusted means from SpATS were used. In traits measured over multiple years, a single year was selected. For example, for budburst, the year that displayed the largest variation between provenances was chosen for the PCA. Biplots were produced to visualise the relationships between traits and the relative performance of the provenances. Finally, scatterplots were produced to give an indication of which provenances perform best for three traits representing budburst, growth (height or diameter) and form or survival (*x*-axis *versus* *y*-axis and symbols divided into tertiles). As survival, growth, form and late-flushing are all important characteristics for selecting seed sources, three traits with a significant provenance test out of these were selected.

Results

Test for provenance effect

The Wald test for provenance showed that provenance effects were significant for all traits (α=0.05), although not for all species-trait combinations (Tab. 2). The estimated means for all provenances and traits are given in Tab. S2-S5 (Supplementary material). Below, the results are described in more detail per trait and species.

Survival

The overall survival rates per species ranged between 0.48 and 0.90 (Tab. S2-S5). Higher survival rates were recorded in the *Fagus sylvatica* trial, with an adjusted trial mean of 90% and a range of 77-96% at the age of 11 years after establishment. The *Alnus glutinosa* and *Quercus robur* trials showed mean survival rates of 73% at 14 years and 57% at 13 years, respectively. The *Betula pubescens* trial exhibited the lowest overall survival rate, with a mean of 48% at 14 years, and none of the provenances exceeding 70% survival. The *Quercus robur, Alnus glutinosa* and *Betula pubescens* trials showed a significant provenance effect for survival rates. Though, pairwise comparisons based on the LSD measure between provenances after correction for multiple testing did not show significant differences in survival rates among provenances. For the *Fagus sylvatica* trial there was no significant provenance effect (Tab. 2).

Growth (height and diameter)

Growth differed between species, with *Alnus glutinosa* displaying the highest growth, achieving a mean height of 10.3 m at age 11 (Tab. S2-S5). This was followed by *Betula pubescens* with a height of 7.4 m at age 12, while *Fagus sylvatica* and *Quercus robur* exhibited the lowest heights of 6.0 m at age 10 and 6.4 m at age 12, respectively. Significant provenance effects for height and diameter were found, except for diameter in the *Alnus glutinosa* trial and for height in the *Quercus robur* trial (Tab. 2). Pairwise differences were most pronounced in *Betula pubescens*, also between autochthonous provenances. Provenance 410 (category SI), attained the highest growth rates with a height of 10.8 m and a diameter of 11.3 cm. The seed orchard trees, included in the trial as two different seed harvest years (403 and 404), ranked among the lowest-performing provenances in growth. In the *Alnus glutinosa* trial, height ranged from 9.5 m (provenance 268) to 10.9 m (provenance 277), with pairwise comparisons indicating non-significant differences between provenances. Autochthonous seed sources generally exhibited growth comparable to provenances categorized as “Selected” and “Tested”. In the *Fagus sylvatica* trial, the three autochthonous seed sources (187, 188, and 189 – category SI) showed the lowest growth performance in both height and diameter, although differences between provenances were not significant after adjustment for multiple testing. Among the *Quercus robur* provenances, the “Selected” and “Tested” categories generally showed the highest diameter growth.

Tab. 2 - Results of the Wald test of provenance effect for the six traits per species. (Trait): each trait-age combination; (Wald Statistics): Wald test for provenance effect; (DF): degrees of freedom; (P-value): Probability value; (*): P < 0.05; (**): P<0.01; (***): P<0.001; (ns): non-significant.

Species	Trait	Wald Statistics	DF	P-value
Quercus robur	Survival13	48.5	15	***
	Budburst6	194.3	15	***
	Budburst7	189.4	15	***
	Budburst8	189.4	15	***
	Height12	21.6	15	ns
	Diameter12	40.4	15	***
	Straightness13	115.2	15	***
	Forks13	15.6	15	ns
Fagus sylvatica	Survival11	20.3	12	ns
	Budburst4	327.1	12	***
	Budburst5	339.4	12	***
	Height10	34.3	12	***
	Diameter10	33.3	12	***
	Straightness11	14.5	12	ns
	Forks11	47.8	12	***
Alnus glutinosa	Survival14	47.9	31	**
	Budburst5	60.6	31	**
	Budburst6	89.1	31	***
	Budburst8	68.5	31	***
	Diameter11	39.2	31	ns
	Height11	61.9	31	***
	Straightness14	85.9	31	***
	Forks14	93.5	31	***
Betula pubescens	Survival14	32.8	13	***
	Budburst6	64.9	13	***
	Budburst7	108.1	13	***
	Budburst8	70.7	13	***
	Height12	174.2	13	***
	Diameter12	259.9	13	***
	Straightness14	20.1	13	ns
	Forks14	15.8	13	ns

Budburst

Budburst scores showed strong correlation between years, particular in *Quercus robur* and *Fagus sylvatica*, indicating high temporal consistency among provenances. For example, for *Quercus robur*, the correlation between 2014 and 2015, and 2015 and 2016 was $r = 0.96$ and for 2014-2016 $r = 0.97$. Less stronger correlations were observed for *Alnus glutinosa* and *Betula pubescens* (Tab. 3). Budburst had a clear provenance effect for all species (Tab. 2), though for *Alnus glutinosa* and *Betula pubescens* provenances, there was minimal variation in budburst. Although statistically significant differences among specific provenances were detected in some years, the mean budburst rates for the provenances fell within a comparable range (*Betula pubescens*: 3.0-3.9 in 2016; *Alnus glutinosa*: 3.5-4.6 in 2015). In contrast, the differences in budburst were more pronounced in the *Quercus robur* and *Fagus sylvatica* trials. Here the later-flushing provenances were typically from autochthonous origin (SI category – Tab. S4-S5 in Supplementary material). In the *Fagus sylvatica* trial, the provenances with later budburst times included the autochthonous provenances 187, 188, and 189 (SI category), followed by the three provenances 177, 178, 179, two of which have the qualification “Tested”. The earliest flushing was observed among the other “Selected” provenances. In the *Quercus robur* trial, the majority of autochthonous provenances exhibited significantly later budburst than the three “Tested” provenances (260, 261, 262 – Tab. S5 in Supplementary material).

Stem straightness and forking

In *Betula pubescens*, no significant provenance effect for straightness ($p > 0.05$) and forking ($p > 0.05$) was detected (Tab. S3). Forking scores ranged from 3.7 to 4.4, and stem straightness scores ranged from 2.6 to 3.1, indicating that most provenances performed well in terms of form. In the *Alnus glutinosa* trial there was a significant provenance effect ($P < 0.001$) for both form traits (Tab. 2). The overall trial mean for forking was 4.4, with small differences among provenances (Tab. S2). For stem straightness, scores ranged from 2.9 to 3.7, with most provenances demonstrating reasonably good straightness, comparable to the provenance 250 (Denekamp-01, cate-

Tab. 3 - Pearson’s correlation coefficient (r) between years for the budburst stage using provenance mean values.

Species	Budburst stage		
	year 1 × year 2	year 2 × year 3	year 1 × year 3
Alnus glutinosa	0.67	0.5	0.59
Betula pubescens	0.52	0.85	0.57
Fagus sylvatica	1	-	-
Quercus robur	0.96	0.96	0.97

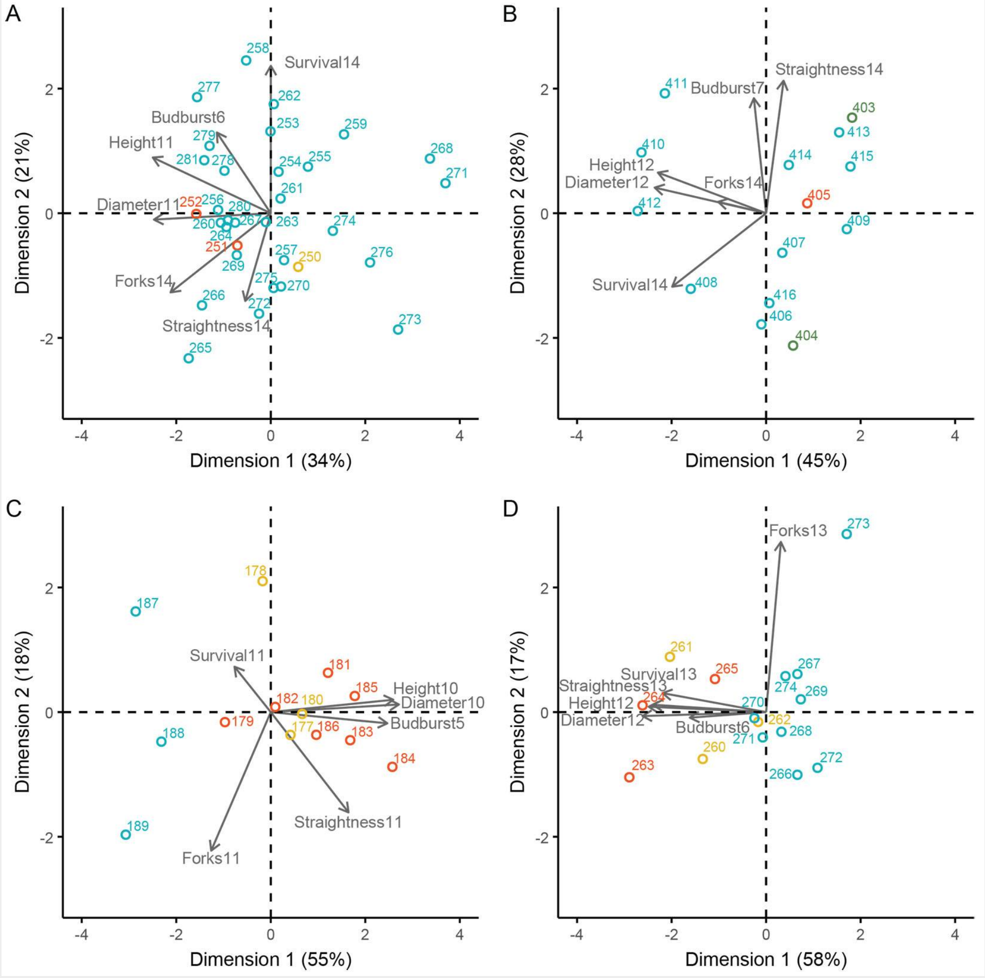


Fig. 2 - Plots of provenance scores for principal components 1 and 2 (PC1 *vs.* PC2) for the four species. The color of the points represent the category of FRM of the provenance (SI = blue, S = red, T = yellow, Q = green). The vectors correspond to the direction and contribution in the plot of the six traits. For provenance IDs and trait abbreviations see Tab. 2 and Tab. S1 in Supplementary material. (A) *Alnus glutinosa*, (B) *Betula pubescens*, (C) *Fagus sylvatica*, (D) *Quercus robur.*

gory "Tested"). Only, four autochthonous provenances (255, 259, 271, 278) exhibited significantly poorer straightness than Denekamp-01 (Tab. S2 in Supplementary material). In general, the forking scores in the *Quercus robur* and *Fagus sylvatica* trials were lower than those observed in the *Alnus glutinosa* and *Betula pubescens* trials. In the *Quercus robur* trial, with scores for forking ranging from 2.7 to 3.8, no significant provenance effect was detected (Tab. S5). Concerning straightness, differences were more pronounced, with the "Tested" and "Selected" provenances ranking among the highest. The straightness scores for the autochthonous provenances varied, ranging from 3.1 (provenance 270) to 2.0 (provenance 275), the latter being the least straight. In the *Fagus sylvatica* trial, a provenance effect was observed for forking but not for straightness (Tab. 2). The mean forking score across all provenances was 2.7 (Tab. S4). Also, the overall mean for straightness across provenances was relatively low (2.7) and no significant differences between provenances were found (Tab. S4 in Supplementary material).

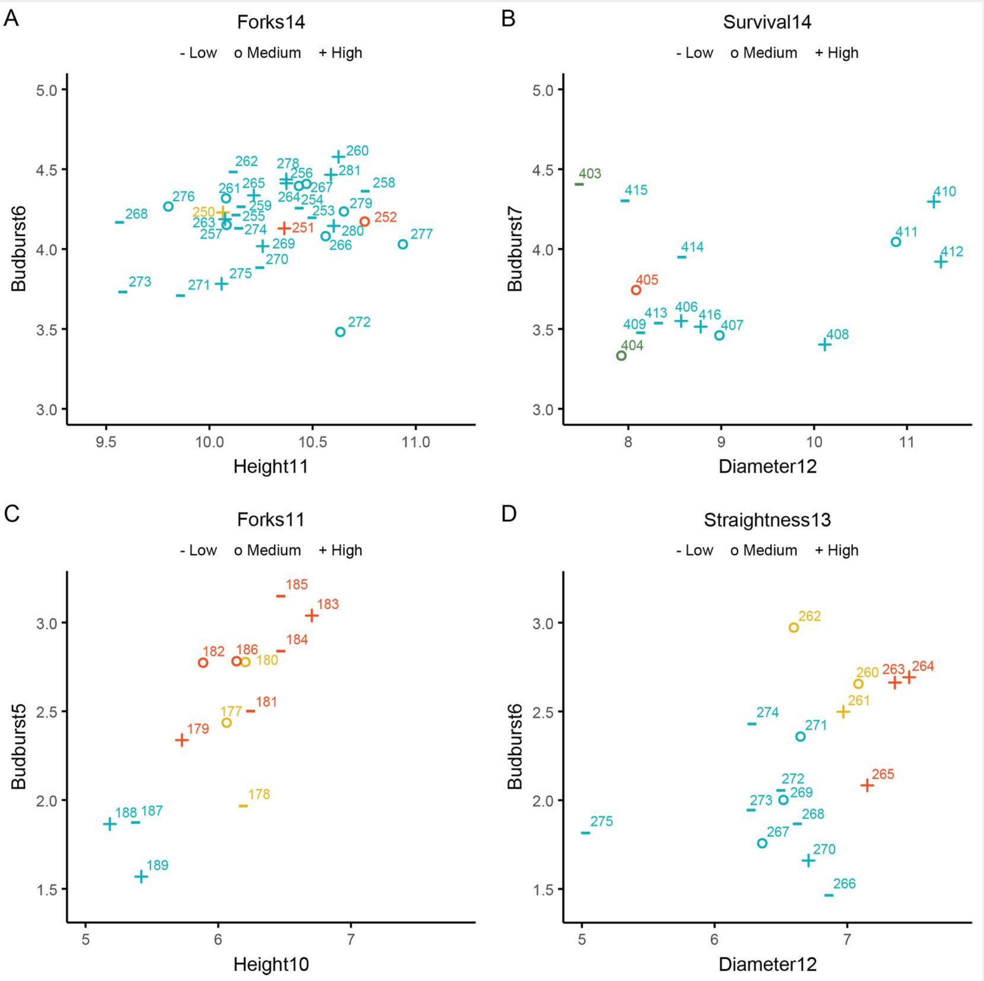
PCA of all traits

The results of the PCA indicated that growth traits (height and diameter) along the first principal component (PC1) had the most significant influence on determining variation among provenances for all species (Fig. 2). In the case of *Alnus glutinosa*, the first two principal components explained 55% of the total variation, with PC1 accounting for 33.7% and PC2 for 21.3% (Fig. 2A). The analysis demonstrated that provenances exhibiting good growth and early budburst were distinguished along the *x*-axis from those with lower growth performance and later flushing. Along PC2, negatively correlated vectors for straightness and survival were found (Fig. 2A). In *Betula pubescens*, the first two principal components accounted for 72.2% of the variation (PC1 = 44.5%, PC2 = 27.7% – Fig. 2B). The second component was primarily explained by straightness and budburst, with a high straightness being associated with early budburst. For *Fagus sylvatica*, PC1 accounted for 54.9% of the total variation, indicating that provenances with high growth also exhibited early budburst (Fig. 2C). The second component accounted for 17.9% of the variation, where straightness and forking were most important. In *Quercus robur*, the first two components explained 74.3% of the variation (PC1 = 57.7%, PC2 = 16.6% – Fig. 2D). The second component was mainly associated with forking, which did not correlate with any of the other traits (Fig. 2D).

Selecting provenances

For all species, height and diameter were highly correlated. Additionally, the form traits straightness and forks were correlated with each other, except in the *Quercus robur* trial. For all species, one of the growth traits was consistently included as one of the traits (*x*-axis), along with budburst (*y*-axis). The third trait varied across species. Fig. 3C shows that for *Fagus sylvatica*, provenances demonstrating superior height growth often have earlier budburst. The autochthonous provenances (cat. SI) are in the lower-left quadrant of the plot, indicating they are later flushing but also have less growth. Forking does not correspond with this relationship, as provenances with high fork class scores (represented by red dots) show varied growth and budburst patterns. In *Quercus robur*, unlike in *Fagus sylvatica*, provenances with higher growth (as indicated by diameter) do not have earlier budburst. Autochthonous provenances, most of which flush later, do not cluster in the lower-left quadrant of the plot, but instead exhibit different diameter growth values. Provenances in the category "Selected" and "Tested" are in the upper right quadrant of the plot, indicating that they have in general higher growth and are earlier flushing. Moreover, the coding (plus sign) for straightness sug-

Fig. 3 - Scatter diagrams of the four species. (A) *Alnus glutinosa*, (B) *Betula pubescens*, (C) *Fagus sylvatica*, (D) *Quercus robur*. Numbers represent provenance IDs. The color of the symbols represent the category of FRM of the provenance (SI = blue, S = red, T = yellow, Q = green). For provenance ID codes and trait abbreviations see Tab. 2 and Tab. S1 in Supplementary material. Higher values for budburst indicate earlier budburst.



gests they also perform best for straightness. Provenance 275 exhibits remarkably low rates for the combination of diameter growth and straightness compared to the other provenances, while the two autochthonous provenances 265 and 270 perform well for all three traits (Fig. 3D). In the case of *Alnus glutinosa*, provenances are scattered throughout the plot. It also shows that many taller provenances had also earlier budburst. The "Tested" provenance 250 (Denekamp-01) is situated in the centre for growth and budburst, but with higher forking performance. The scatterplot also shows that there are several autochthonous provenances that perform similar or better than Denekamp-01 for all three traits (for example 263, 269, 275, 280). For *Betula pubescens*, the plot illustrates that provenances with larger diameters also tend to have higher survival rates, but differ in budburst. The seed orchard seed lots (403, 404) and the "Selected" provenance 405 are among the worst performers.

Discussion

Variation in survival and growth

Significant provenance effects for survival were observed in *Quercus robur, Alnus glutinosa* and *Betula pubescens*, but not in *Fagus sylvatica*. Also, survival rates varied among species, with *Fagus sylvatica* exhibiting the highest survival (trial mean 90%) and *Betula pubescens* the lowest (48%). This suggests that *Fagus sylvatica* may be better suited to the trial site conditions. Knowing that birches are sensitive to transplanting (Barnes & Percival 2006), the lower survival in *Betula pubescens* is probably partly due to a transplanting shock. *Betula pubescens* trees have a preference for cool, moist soils but face challenges in hot, dry conditions due to their shallow root systems (Niinemets & Valladares 2006, Beck et al. 2016). Due to their shallow root system, also site-specific management issues such as competition with vegetation can play a role. In contrast, the open conditions of a provenance trial may not reflect the natural forest environment where this species typically thrives.

Growth differences (height or diameter) were found in all species, but the most pronounced provenance effect was observed in *Betula pubescens*, where the tallest provenance was nearly twice as tall as the shortest, a height difference of 5.2 meters at age 12. Interestingly, four of the eleven autochthonous provenances (cat. SI) in this species outperformed seed orchard and "Selected" materials. In the other species pairwise comparisons showed that autochthonous provenances (cat. SI) exhibit in many cases comparable growth as provenances in the higher categories (S and T). These findings suggest potential for selection within "Source identified" material to use for forests with wood production function.

Differences in spring leaf phenology

Significant provenance effects for budburst were evident in all four species, with the clearest differentiation in timing of budburst and consistency over years observed in *Fagus sylvatica* and *Quercus robur*. Autochthonous *Fagus sylvatica* provenances and most autochthonous *Quercus robur* provenances showed the latest budburst among the studied provenances. This is noteworthy since the "Tested" *Fagus sylvatica* provenances (177, 178 and 180) and in particular the "Tested" oak provenance Ede-01 (260), which is an accepted standard, were in earlier trials explicitly selected for their relatively late budburst (Kranenborg & De Vries 1999, 2001, Kranenborg et al. 2010). However, in these trials seed sources were recommended as "Tested" based on comparisons with seed sources from 20th century plantation forests and roadside plantations, and occasionally foreign material (Kranenborg & De Vries 2001), but not with autochthonous seed sources. Late budburst is generally expected in Dutch autochthonous populations due to local adaptation, as delayed flushing reduces the risk of frost damage (Hänninen 1991, Von Wuehlisch et al. 1995). In the Netherlands late frost events occur occasionally, which makes late budburst an important selection criterium for these species. On a broader range-wide scale, longitudinal trends in *Fagus sylvatica* budburst have been observed, with Northern and Western European provenances generally flushing later than those from Southeast Europe (Von Wuehlisch et al. 1995, Jazbec et al. 2007, Gömöry & Paule 2011, Robson et al. 2013). In these European-wide trials Dutch autochthonous *Fagus sylvatica* provenances (*e.g.*, Aarnink, Elspeet) have consistently been recorded as among the latest to flush (Gömöry & Paule 2011, Robson et al. 2013, Eilmann et al. 2014). Similarly, Dutch *Quercus robur* provenances also exhibit late flushing in comparisons of provenances at a regional scale across Northwestern Europe, as confirmed in provenance trials in Ireland (Felton & Thompson 2008), Denmark (Jensen & Hansen 2008) and Southern England (Wilkinson et al. 2017). For *Quercus robur,* Wilkinson et al. (2017) found that the southern provenances were always earlier than those from more northern latitudes. For *Alnus glutinosa* and *Betula pubescens* differences between provenances were less pronounced. Early successional species, such as *Alnus glutinosa* and *Betula pubescens*, generally have earlier budburst than the mid- to late-successional species *Quercus robur* and late-successional *Fagus sylvatica* (Chamberlain et al. 2021). Despite its early budburst, *Alnus glutinosa* is reported to be relatively tolerant to spring frost (Vares et al. 2004, Claessens et al. 2010). Therefore, the selective pressure of spring frost on populations in this species may be weaker than in more frost-sensitive species, leading to less differentiation in budburst timing among provenances. Moreover, budburst was not considered in the only provenance trial of *Alnus glutinosa* previously conducted in the Netherlands (Verwey 1977). Apparently, budburst was not seen as an important trait to select for, while good growth and stem form were. Neither is there much literature on provenance differences for budburst on European or regional scale. Baliuckas & Pliura (2008) assessed budburst of *Alnus glutinosa* in field trials located in different eco-geographic regions of Lithuania, finding a southeast-northwest clinal variation pattern. Though, the most comprehensive common garden experiment performed in Pennsylvania (USA) with 48 *Alnus glutinosa* provenances from the European range, showed that populations were rather uniform in budburst timing and no clear pattern of climate differences was detected (DeWald & Steiner 1986). Studies for *Betula pubescens* are even scarcer. Billington & Pelham (1991) examined seven natural Scottish *Betula pubescens* populations in a single progeny test and found significant differences among populations and among families within populations.

Provenance differences at a small geographic scale

Despite the small geographic scale of our sampling, using provenances sourced exclusively from the Netherlands, we detected modest, yet significant provenance effects across most species-trait combinations, highlighting genetic differentiation even within a relatively climatologically and ecologically uniform lowland area as the Netherlands. While local adaptation was not assessed, the observed genetic differentiation in budburst and growth, both key adaptive traits, at such a small geographic scale is interesting. Adaptive genetic differentiation in European forest species is driven by environmental gradients such as temperature, precipitation, soil composition, and altitude. The Netherlands lacks substantial environmental gradients, as climatological or altitudinal variation is low, comparable to the lowland regions of Belgium (Flanders) or Denmark. Indeed, De Kort et al. (2014) analyzed *Alnus glutinosa* populations in conventional provenance trials combined with population genomics but found very limited evidence of adaptation at the scale of Belgian provenance regions. On the other hand, Jensen (2000) demonstrated that even within the relatively small region of Jutland, significant genetic variation in flushing time exists among native oak provenances, strongly influenced by proximity to the coast. In another study in Denmark, Lobo et al. (2018) found genetic differentiation at a fine scale in phenology in six woody species, including *Betula pubescens*. They demonstrated that local populations can be genetically differentiated, even when separated by distances of only 10 to 35 km, in areas with low altitude variation and spring temperatures that vary by only 1 °C to 2.5 °C. As the observed variation could only be partly explained by the climate at the site of origin, they suggested it is likely a product of both natural selection and non-adaptive forces. Such a similar explanation might be given for the results of the Dutch provenances, where even without strong selective pressures, natural processes such as restricted gene flow, historical events, and random genetic drift might have contributed to the observed differentiation at such small geographic scale.

Historical management effects on stem form

Due to past management practices, such as coppicing, most autochthonous Dutch seed sources have been considered inferior in stem quality. As these stands cannot be visually selected for their phenotypic superiority, their Forest Reproductive Material is classified as "Source identified" and not as "Selected". However, our findings indicate that under trial conditions, several of these autochthonous provenances have the potential to produce high-quality stems comparable to provenances used as standards, suggesting their suitability for production purposes. It is important to recognize that these trials are still in their early stages, and assessing form characteristics at age 11-14 may be premature. For fast-growing pioneer species such as *Alnus glutinosa*, as well as *Betula pubescens*, which are short-lived species, this age might be sufficient. However, for slower-growing and long-living species like *Quercus robur* and *Fagus sylvatica*, which develop their final stem quality later, these form assessments may be relatively early to give reliable conclusions.

Practical implications for seed sourcing

Provenances that exhibit a combination of desirable traits, including good growth, late flushing, good stem form and high survival rates, are the most suitable for Dutch forestry with a production-oriented objective. The autochthonous provenances included in this study are among the first to be evaluated for these traits. Our results suggest a correlation between growth and timing of budburst, particularly in *Fagus sylvatica*. Here, the best-growing provenances also exhibited earlier budburst, potentially complicating the selection of provenances that optimize both traits. Several studies on *Fagus sylvatica* have shown that, in certain parts of its range, late budburst – an adaptive strategy to avoid late frosts – has been linked to reduced height growth (Gömöry & Paule 2011, Robson et al. 2013, Delpierre et al. 2017). Based on our findings, we propose recommendations for seed sourcing, in particular to register certain autochthonous (category SI) provenances for production purposes. Given the anticipated increase in demand for planting stock in the Netherlands, we recommend prioritizing the highest-performing SI provenances for seed harvesting when wood production is a key objective. Conversely, lesser performing autochthonous SI provenances should be avoided or only harvested in cases where biodiversity conservation or landscape restoration is the priority in the plantings. Additionally, increased harvesting in autochthonous stands requires careful consideration of genetic diversity, as some of these forests are small remnants. To ensure a genetically diverse and resilient seed supply, for small stands, mixing of SI seed sources with similar characteristics could be considered.

Conclusions

Our study demonstrates that even at a small geographic scale, local seed sources exhibit genetic differences in spring leaf phenology, growth, and form traits. Budburst, a key adaptive trait in frost-prone regions like the Netherlands, varied significantly, particularly in *Fagus sylvatica* and *Quercus robur* with autochthonous sources generally flushing among the latest. The results also demonstrate that several autochthonous seed sources showed good stem form, despite past coppicing, indicating their potential for use in production forestry. This was evident in all species. We identified provenances in each species that combine favorable traits such as good growth, acceptable form, high survival, and late budburst. These findings support the registration and use of certain autochthonous local seed sources for both timber production and ecological purposes. The results cannot be directly extrapolated to inform provenance selection for other planting sites. Studies indicate that site effects often have a greater impact than provenance effect (Sáenz-Romero et al. 2017, Rosique-Esplugas et al. 2022, Unterholzner et al. 2024). However, the test sites reflect typical growing conditions for the four species in the Netherlands, which is a single provenance region, characterized by minimal climatological or ecological variation. Thus, our recommendations for seed sourcing can be broadly applied across the country. Nevertheless, soil characteristics remain a critical factor as shown by Buras et al. (2020), who found soil-type-specific growth patterns in *Quercus robur* provenances. Future research should prioritize multi-site trials that incorporate diverse soil types to further refine provenance recommendations.

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Supplementary Material

Tab. S1 - Overview of provenances tested in the trials and background information.

Tab. S2 - Estimates of provenance values (adjusted means) for *Alnus glutinosa*.

Tab. S3 - Estimates of provenance values (adjusted means) for *Betula pubescens*.

Tab. S4 -Estimates of provenance values (adjusted means) for *Fagus sylvatica*.

Tab. S5 - Estimates of provenance values (adjusted means) for *Quercus robur*.

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