Effects of seed origin on the growth and stem quality of wild service tree (*Torminalis glaberrima* (Gand.) Sennikov & Kurtto)

Evaluating survival, growth, and stem quality of nine European seed sources of wild service tree at three locations in southern England four growing seasons after planting

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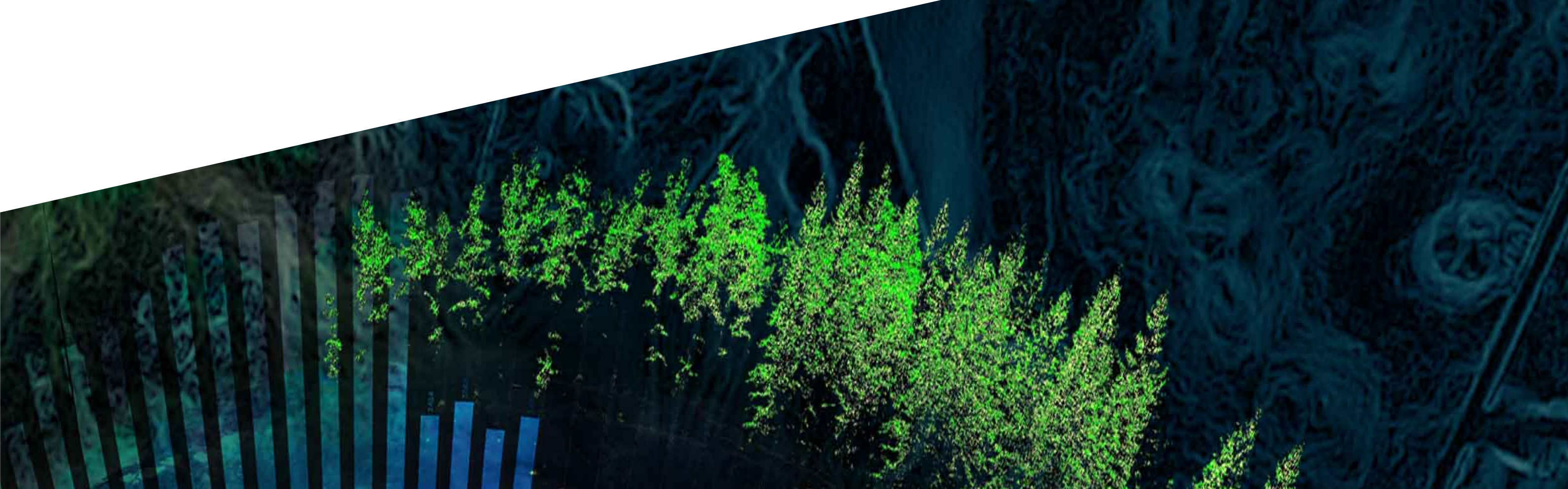

Effects of seed origin on the growth and stem quality of wild service tree (*Torminalis glaberrima* (Gand.) Sennikov & Kurtto)

Effekter av fröursprung på tillväxt och stamkvalitet av tyskoxel (Torminalis glaberrima (Gand.) Sennikov & Kurtto) – Utvärdering av överlevnad, tillväxt och stamkvalitet av nio europeiska frökällor av tyskoxel på tre lokaler i södra England, fyra tillväxtsäsonger efter plantering

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Abstract

The wild service tree *(Torminalis glaberrima)* is a rare, light-demanding broadleaved species valued for its high-quality timber and potential contribution to climate-resilient forestry in Europe. This study presents results from the first seed source trial of the species in England, evaluating nine European seed sources — from England, France, Germany, and Italy — over the first four growing seasons. The wild service tree was planted in a mixed-species design alongside pedunculate oak (*Quercus robur*), field maple (*Acer campestre*), and hornbeam (*Carpinus betulus*). Survival, growth, stem form, crown architecture, and phenology were assessed across three somewhat contrasting sites to identify suitable material for future timber production.

Significant differences were observed between seed sources, with clear evidence of both genetic and site-level environmental influences. Two continental seed sources consistently outperformed the others in growth, stem form, and branching structure. Four seed sources showed intermediate performance with good potential, while three — including all English origins — exhibited slower growth and higher rates of forking and dieback. Site effects were also pronounced, with growth performance strongly linked to soil structure, topography, and early establishment management.

Phenological observations revealed distinct genetic patterns in spring flushing and autumn dormancy, with the top-performing continental seed sources exhibiting earlier bud burst and longer growing seasons. While this trait may enhance growth under mild conditions, it also implies an increased risk of frost damage — although no such damage was observed during the study period. Crown architecture and pruning requirements were closely linked to growth and stem form, underscoring the importance of integrated selection criteria when evaluating seed source performance.

The results indicate potentially promising seed sources for high-quality timber production under southern English conditions and provide early evidence of the species' silvicultural potential. Continued monitoring, expanded geographic testing, and targeted breeding efforts are recommended to support the broader deployment of wild service tree in climate-resilient forestry strategies.

Keywords: Minor tree species, climate & site adaption, high-quality timber production, *Sorbus torminalis*

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Abbreviations and symbols

CEC	Cation exchange capacity
CRPF	Centre Régional de la Propriété Forestière
CV	Coefficient of variation
DBH	Diameter at breast height
DTB	Diameter of thickest branch
L-P-C	Lugny-Plottes-Chardonnay
MAI	Mean annual increment
ONF	Office National des Forêts
REML	Restricted maximum likelihood
SNP	Single nucleotide polymorphisms
SSR	Simple sequence repeats
WST	Wild service tree

1. Introduction

1.1 Background

Wild service tree (*Torminalis glaberrima* (Gand.) Sennikov & Kurtto) is among Europe's rarest broadleaved tree species (Kleinschmit, 1998), it is drought tolerant and thrives in warm sites. Studies suggest that predicted climate changes could expand its distribution and enhance its future role in silviculture (Walentowski *et al*., 2017; Kunz *et al.,* 2016, 2018; Schmucker *et al.,* 2023; Dyderski *et al.,* 2024).

Climate change is projected to increase the frequency of extreme weather events, such as storms and droughts, while also elevating the risk of pathogenic outbreaks, emphasizing the need for alternative tree species to diversify risks in silviculture (Eyring *et al.,* 2016; Thurm *et al.,* 2018; Zscheischler and Seneviratne, 2018; Spinoni *et al.,* 2019; Cook *et al.,* 2020; Ionita and Nagavciuc, 2021). The rate of climate change may also exceed the adaptive capacity of certain tree species, limiting their ability to naturally adjust to new habitats (Jump and Peñuelas, 2005). Assisted migration of tree species (Williams and Dumroese, 2013; Dumroese *et al.,* 2015) and assisted gene flow among populations (Aitken *et al.,* 2008) are strategies to introduce tree species or populations to locations where future climatic conditions are expected to be suitable.

Interest in the wild service tree has grown in recent decades due to its drought tolerance, ecological values and aesthetics. The timber is also highly appreciated, its rarity has led to record prices for high-quality veneer, making it one of the most valuable hardwoods in Europe (Skovsgaard and Graversgaard 2013a; Kunz *et al.,* 2018; Werres, 2018).

Despite this, research-based knowledge about its growth characteristics, particularly concerning seed origin and environmental factors, remains limited compared to more common species. The wild service tree has a broad yet fragmented distribution, occurring in lowland to sub-alpine conditions *(Fig. 1).* Its ability to grow across diverse site conditions suggests genetic variation among provenances. Transplanting trees from southern to northern latitudes can enhance growth due to longer growing seasons in their native habitats. However, growth rate, stem quality, and site adaptability may differ substantially between provenances. Understanding how different genetic origins respond to varying site conditions is critical for successful establishment and potential future tree breeding programs.

1.1.1 Objective

To address these knowledge gaps, a field trial was established in autumn 2019, testing nine European seed sources of wild service tree at three locations in England. The trial is intended to run for a full rotation period to assess the development of these seed sources in this region and improve silvicultural methods (Guest and Skovsgaard, 2021). Additionally, the trial sites could serve future tree breeding programs (Forestry Commission, 2023). The wild service trees will be studied for survival, growth, and stem quality to identify the most suitable seed sources for high-quality timber production. This is the first wild service tree provenance trial in England and one of few active wild service tree provenance trials in Europe with a focus on high-quality timber production.

This thesis aims to provide insights into the growth and stem quality characteristics of previously unstudied provenances of this rare tree species, which could gain importance in future silviculture. Although still in the early stages, this study offers an initial indication of which seed sources are most promising for high-quality timber production and potential future tree breeding efforts in southern England and regions with similar site conditions.

The research questions guiding this thesis are:

1. Which seed sources appears most suitable for high-quality timber production at this stage?
2. Is there a difference in performance between sites, and what factors contribute to these differences?
3. Do southern seed sources exhibit higher growth rates and/or longer growing seasons?
4. Can this knowledge be applied to southern Scandinavia or similar regions at the northern distribution range?

Understanding the growth and stem quality characteristics of different provenances of the wild service tree is crucial for selecting suitable planting material in a changing climate. This study aims to provide knowledge that could enhance the species' role in future silviculture, particularly in regions like southern England and southern Sweden, where alternative species can diversify forest composition and mitigate climate-related risks.

In this study, the term provenance refers to the original geographic area from which trees originate. In contrast, seed source represents the location where seeds were collected, which may include seed orchards where multiple provenances are mixed or unknown. Since some of the seed sources in this trial originate from French seed orchards, where the individual tree origins are uncertain, the term seed source is used for the studied trees throughout this thesis to maintain clarity.

1.2 Literature review

1.2.1 Previous research on seed origin

The oldest and most documented provenance trial of wild service tree, with attention to growth and quality traits was established in 1979 at three locations in Germany, testing eight European provenances, five German, one French, one Czech and one from Luxemburg. Two trials were planted in Lower Saxony, in Grohnde and Lutter, and one in Baden-Württemberg. The first two are no longer active as trials but are used as seed orchards. The third is planted in the Liliental research forest outside Freiburg im Breisgau, it is still active, and it has been studied for growth and stem quality traits on several occasions. Three of the German provenances from northern Bavaria and the French from Bar-le-Duc performed well and were recommended as planting material, as well as suitable for future tree breeding (Bamberger, 1990; Stannehl, 1993; Kausch-Blecken von Schmeling, 1994; Schüte, 2000; Skovsgaard and Graversgaard, 2013a; Šeho *et al.,* 2018). Sailershausen, one of the best performing provenances in the study, originating from the Würzburg University Forest in northern Bavaria is included in this study.

A progeny trial established in 1995 in Heilbronn, northern Baden Württemberg contains regional seed sources, seven from Baden Württemberg, and one from Alsace, France. It was assessed for height growth and stem quality in 2003 (C. Neophytou, e-mail, 23 August 2024). There are a few other forest trials with wild service tree in Germany, but these are the only two comparing different origins in terms of timber production (Kausch-Blecken von Schmeling, 1994; C. Neophytou, e-mail, 23 August 2024).

In 2022 a seed orchard with 98 clones was established in addition to older seed orchards, it is part of a climate change adaption project with alternative forest tree species in Germany. It is suggested that a new trial containing 10 provenances from an array of the distribution range should be established (Liesebach *et al.,* 2021). Baier *et al.* (2017) have based on phenotypic assessments and genetic studies, identified 26 harvest, 7 development and 5 genetic conservation stands, divided in four areas of origin with a similar spatial-genetic population structure, in Bavaria and Baden-Württemberg.

A series of provenance trials were performed in France between 1997 and 2008 containing seeds harvested from 31 locations in France. However, the study was mainly focused on genetic diversity, hence the trees were not selected based on stem quality, branching or vigour (Planfor, 2013; S. Muratorio, e-mail, 29 February 2024). A study on chloroplast DNA (Demesure *et al.,* 2000) showed very little differentiation and geographical structuring of the species in Europe. As a result, two French regions of origin were defined based on ecological and climatic data, the north of France (STO901) and the south-west and Mediterranean region of France (STO902).

In Poland a provenance trial was established in 2012 with seed collected from ten Polish populations. Growth and stem quality characteristics as well as genetic variability were studied, seven provenances were recommended for future plant propagation (Sułkowska and Wojda, 2015; Sułkowska *et al.,* 2021).

A provenance trial in Switzerland, containing 18 species from various provenances was initiated in 2017. The goal of the project is climate change adaption, 57 trial sites was established throughout Switzerland during 2020-2023. The trial contains six provenances of wild service tree, two French, one Italian, one Polish, one Spanish, and one Swiss as a reference (Frei *et al*., 2018, 2024; WSL, 2024).

Studies in northern Iran have been performed on regional seed sources testing germination rate, survival, and growth at a nursery level (Tabandeh *et al.,* 2007; Espahbodi *et al.,* 2007, 2008).

It is possible that there are more provenance trials of wild service tree, but no publications could be found within the scope of this thesis. The rising demand for tested high-quality planting material, suitable for timber production, increases the importance of finding and preserving populations with suitable characteristics.

1.2.2 Species characteristics

Wild service tree, scientifically formerly known as *Sorbus torminalis* (L.) Crantz is now considered to form its own monophyletic group *Torminalis* (Ferrer-Gallego, 2024), it is also known as chequers tree or Swiss pear tree. It is a post-pioneer species, light-demanding but semi-shade tolerant and often occurs in forest edges and openings, or as a subcanopy tree or shrub species (Kausch-Blecken von Schmeling, 1994).

Distribution, reproduction and genetics

Wild service tree has a wide distribution across Europe and parts of western Asia and northern Africa *(Fig. 1),* ranging from southern Denmark and the southern British Isles in the northwest, to Morocco and Algeria in the southwest, and extending eastwards through the Caucasus Mountains and northern Iran. In the north, it is primarily a lowland species (Rasmussen and Kollmann, 2007; Rich, 2010), whereas in southern and southeastern parts of its range it occurs at elevations between 100 and 1,000 m, reaching up to 2,300 m in the Caucasus and Iran (Wohlgemuth, 1993; Dinca, 2000; Tabandeh *et al.,* 2007).

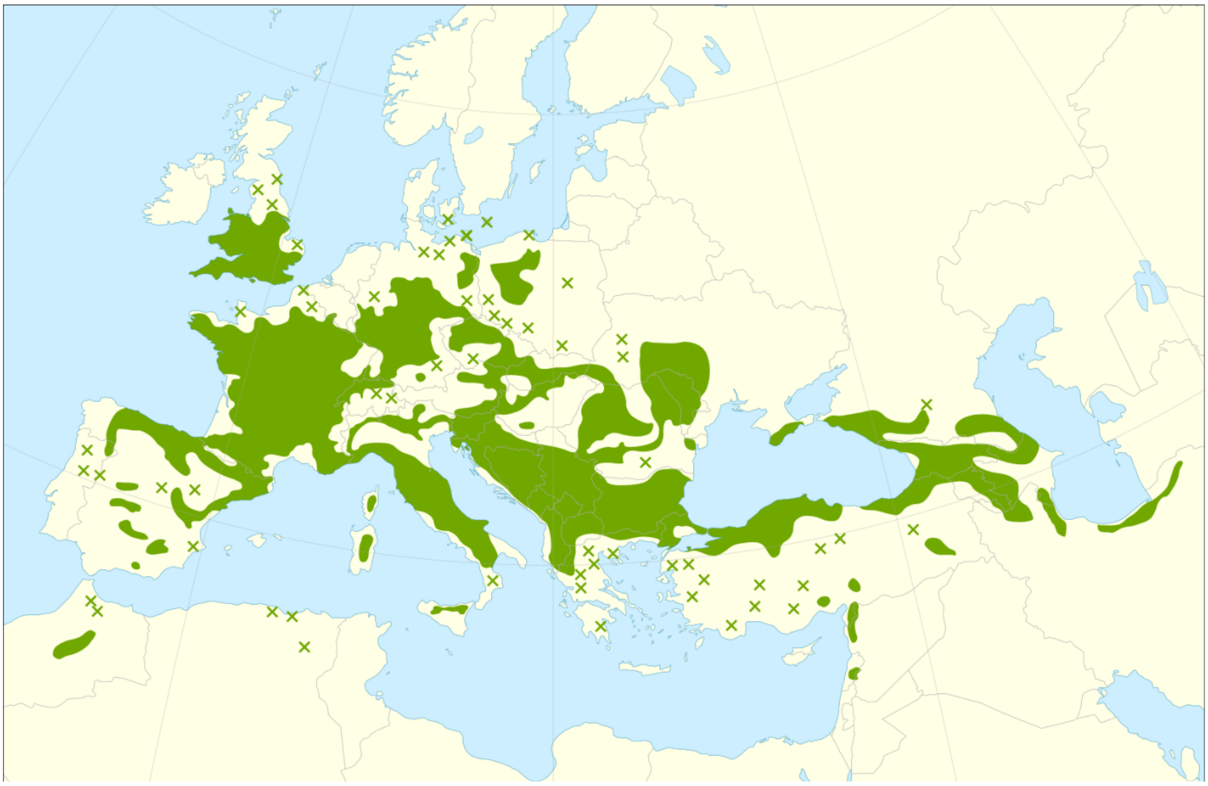

Figure 1. The species is widely but patchily distributed across Europe, western Asia, and parts of North Africa. Isolated populations (X) reflect its scattered occurrence, particularly at the margins of its range. Data from Caudullo et al. (2017).

Despite its broad range, the species is typically scattered in isolated populations due to its weak competitive ability, shade intolerance, and specific habitat requirements. It most often occurs in mixed deciduous forests on nutrient-rich, well-drained soils, and rarely in monocultures (Kausch-Blecken von Schmeling, 1994). Its distribution centre lies in France and southwestern Germany, with particularly high densities east of Paris and throughout the Burgundy and Lorraine regions (Drapier, 1993a; Caudullo *et al.,* 2017).

There is growing evidence that the present-day distribution of wild service tree has been shaped by both natural processes and human activities. The species has long been associated with traditional medicine — its Latin name *Torminalis* refers to its use in treating colic (Grigson, 1955) — and coppice forests where it likely benefited from open canopy conditions (Lloyd, 1977). Human-mediated planting may have increased its frequency on productive sites in lowland Europe (Szymura, 2012), while the transition from coppice to high-forest systems in the 19th and 20th centuries likely contributed to population fragmentation (Thomas, 2017). Genetic analyses show extensive pollen flow at the local scale, but limited evidence of long-distance human-mediated gene flow, except in areas with intensive historical planting (Demesure-Musch and Oddou-Muratorio, 2004).

The wild service tree reproduces both sexually and clonally. Its hermaphroditic, insect-pollinated flowers support an outcrossing mating system, and seeds are dispersed primarily by birds and mammals (Kollmann and Schill, 1996). Seed production is highly dependent on climatic conditions (Termena, 1972). At the northern edge of the range, cool summers are a major limiting factor (Drapier, 1993a; Roper, 1993), while in the southern parts, the distribution is constrained by drought stress exacerbated by high summer temperatures (Drapier, 1993a). Natural regeneration is often sparse, and germination is limited by factors such as low seed viability, thick endocarps, and specific stratification needs (Meier and Leinemann, 2015).

Genetic studies using isozyme and microsatellite markers confirm that wild service tree maintains high genetic diversity between populations across its range (Finkeldey *et al.,* 2000; Oddou-Muratorio *et al.,* 2001b; Thomas, 2017). However, this diversity shows a clear latitudinal gradient: populations in central France exhibit high within-population diversity due to larger population sizes and more gene flow, while northern populations are genetically more isolated, with lower within-population diversity but greater differentiation among populations (Rasmussen and Kollmann, 2008). In parts of Germany and Switzerland, small population sizes (<100 individuals) have contributed to elevated inter-population variation through limited gene flow and genetic drift (Biedenkopf, Ammer and Müller-Starck, 2007).

This geographic pattern is important for conservation and forest management. Isolated northern populations may benefit from increased connectivity or enrichment planting to maintain adaptive potential (Hoebee *et al.,* 2007). At the same time, care must be taken when introducing non-local seed sources, to avoid disrupting locally adapted gene pools. Ex situ conservation efforts, such as seed orchards and controlled breeding programmes, are increasingly recognised as important tools for safeguarding the species' genetic resources in the face of climate change (Aravanopoulos *et al.,* 2015).

Site conditions & ecological requirements

Wild service tree is a thermophilic species, capable of establishing and persisting on dry, rocky, calcareous soils where more competitive species, such as European beech *(Fagus sylvatica L.)* are typically excluded (Rodwell, 1991; Rasmussen and Kollmann, 2008; Fady and Conord, 2010). It performs best in areas with mean annual temperatures between 6.5–17 °C, with an optimum around 8.5 °C, and annual precipitation ranging from 600–1,500 mm, with optimal growth often observed below 800 mm (Wohlgemuth, 1993; Pleines, 1994; González, Rey de Viñas and Cisneros, 2003; Rasmussen and Kollmann, 2004; Oria de Rueda, 2008).

At the northern and eastern edges of its range, the species is typically restricted to south-facing slopes with warmer microclimates (Dinca, 2000). Conversely, in the southern parts of its range — where summer droughts and high temperatures are more limiting — wild service tree is often found on more humid, north-facing slopes (De Dominicis and Barluzzi, 1983). Slope inclination also plays a role; on wetter soils, the species is usually confined to steeper, better-drained sites (Wohlgemuth, 1993).

Although wild service tree can tolerate a wide range of soil types and pH levels (3.5–8), it tends to perform best on slightly acidic to basic soils (Favre-d'Anne, 1990; Lanier *et al.,* 1990; Savill, 1991; Leuschner *et al.,* 2009). It also tolerates a broad range of soil fertility — from nitrogen-deficient to moderately fertile — including humus- and loess-enriched substrates (Madera *et al.,* 2013). The species thrives on moderately dry to very dry sites (Grundmann and Roloff, 2009), can survive short-term flooding, but is intolerant of permanently waterlogged or peaty soils (Madera, Tichá and Repka, 2013).

Despite this tolerance, the best growth performance is observed on deep, fertile soils, particularly those rich in clay or limestone. Optimal individuals are often found on deep, nutrient-rich clays and in river valley bottoms with stable water availability (Kausch-Blecken von Schmeling, 1994; Paganová, 2007; Madera, Tichá and Repka, 2013). Its common association with dry calcareous sites likely reflects its superior drought tolerance compared to canopy dominants such as beech (Pietzarka *et al.,* 2009).

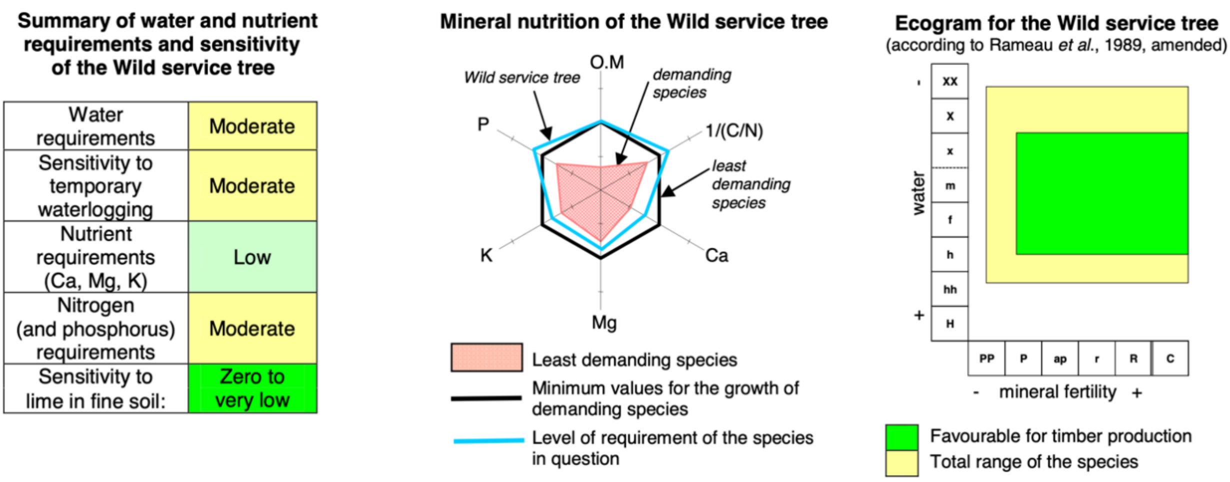

Figure 2. Summary of site requirements for wild service tree (Gonin et al., 2017).

Wild service tree is a relatively poor competitor, particularly under shaded conditions. It exhibits some shade tolerance during its juvenile stage — up to 10 years — but gradually becomes more light-demanding with age (Orsanić *et al.,* 2009). It can persist under dense canopies for extended periods, particularly in mixed broadleaved or oak-dominated forests (Nicolescu *et al.,* 2009) and may survive for decades in the shade of mature oaks (Pyttel *et al.,* 2013). As such, it is best classified as a second-storey or subcanopy species. However, prolonged shading stalls height development and results in plagiotropic, light-seeking crowns that negatively impact timber quality. It responds well to canopy openings and release treatments. Height growth can resume vigorously following crown release, even in older suppressed individuals — a trait known as "growth elasticity" (Pyttel *et al.,* 2013, 2019). This capacity makes it particularly suitable for mixed-species management systems with selective thinning and gap dynamics.

Longevity varies across the species' range. In the northern and eastern parts of its central distribution, wild service trees typically reach 100–200 years of age (Haralamb, 1967; Stănescu, Şofletea and Popescu, 1997; Rasmussen, 2007). In contrast, in more favourable conditions in western and central Europe, individuals can live 200–400 years or more (Crave, 1985; Drapier, 1993a; Roper, 1993; Hurt and Kantor, 2004).

Growth characteristics

The wild service tree is often described as rather fast growing in the early years after establishment compared with related forest species such as, *Quercus robur*, *Carpinus betulus*, and *Prunus avium.* It generally reaches annual height increments of 20–100 cm in the first 10–18 years, declining to 15–25 cm year^{-1} at around 50 years old, to only grow around 5 cm year^{-1} at 70 years old (Röhrig, 1972; Crave, 1985; Bamberger, 1990; Schüte, 2001; Kahle, 2004).

The stem diameter increment is also affected by site conditions and light availability, annual ring width may be as low as 1–2 mm year^{-1}in woodland, while trees growing in open conditions can have increments of 25–40 mm year^{-1}. (Sevrin and Keller, 1993; Hochbichler, 2003; Kahle, 2004; Sjöman *et al.,* 2012). With favourable site conditions, intermediate aged trees can reach an annual increment of around 5.6–7.4 mm year^{-1} (Bastien, 1997).

The diameter increment is also largely affected by age, a study in south-western Germany found that wild service trees growing in a sessile oak-dominant forest had an annual radial increment of 19–22 mm year^{-1} during the first 8 years after establishment, to then decrease at the age of around 25 years, with a constant increment of around 0.7 mm year^{-1} thereafter (Pyttel *et al.,* 2013).

It generally grows to 15–20 meters tall (Favre-d'anne, 1990; Pleines, 1994; Hochbichler, 2003), at the best suitable sites individuals up to 33 metres have been documented (Kausch-Blecken von Schmeling, 1994). The breast height diameter (DBH) usually reaches around 50–90 cm (Jacquot, 1931; Becker *et al.,* 1983; Savill, 1991; Drapier, 1993a; Kausch-Blecken von Schmeling, 1994; ONF, 1999).

One of the thickest documented wild service trees is located south of Aarhus, Denmark, with a DBH of approximately 150 cm (Skovsgaard and Graversgaard, 2013b), which also makes it one of the most northern ones.

Pests and pathogens

Wild service tree is generally considered a resilient species with limited reports of severe pest and disease outbreaks compared to other broadleaved species. However, it is not immune to challenges posed by pathogens and insects, which can affect growth, survival, and timber quality, especially under changing climatic conditions.

Several insects and mites can affect its growth and reproduction. Mites such as *Eriophyes torminalis* and *Phytoptus pyri var. torminalis* are specific to the species, while aphids like *Dysaphis aucupariae* can cause leaf deformation and premature leaf fall, particularly in mainland Europe (Lanier, 1993; Ripka, 2010).

Leaf miners, including *Stigmella torminalis* and *Phyllonorycter leucographella*, occasionally affect foliage in specific regions such as Britain and Poland (Emmet, 1976; Walczak *et al.,* 2010).

Seed predators, like the chalcid wasp *(Torymus druparium)*, can severely reduce seed viability, while other pests, such as the pear shoot sawfly *(Janus compressus)*, occasionally causes minor shoot withering but poses no substantial threat to tree health (Coello *et al.,* 2013).

It is susceptible to several fungal pathogens, including *Armillaria spp.,* which can cause fatal infections (Drapier, 1993b). It serves as a minor host for European canker (*Nectria galligena*) and apple scab (*Venturia inaequalis*), while *Verticillium spp.* can lead to branch dieback and wilting (Butin, 1989; Kausch-Blecken von Schmeling, 2000).

Although these pests typically cause localized or minor impacts, severe infestations, particularly by aphids, can reduce tree vigour and productivity. Effective management involves monitoring pest populations and promoting mixed species stands to dilute pest pressure.

Frost, drought and other environmental stressors

Wild service tree is rather tolerant to environmental stressors but remains vulnerable during certain stages of growth. Seedlings are susceptible to frost damage, though saplings and mature trees, once cold-hardened, can withstand temperatures as low as −31 to −34 °C (Haralamb, 1967). However, spring and early autumn frosts can kill unhardened buds, often resulting in forking and the development of co-dominant shoots (Pietzarka, Lehmann and Roloff, 2009).

It has a high drought tolerance, surviving dry periods lasting several months due to partial isohydric stomatal control (Ellenberg, 1988; Martínez-Vilalta *et al.,* 2002). Prolonged drought can lead to foliar senescence, reduced growth, and increased susceptibility to pests and diseases (Hemery *et al.,* 2009). Short-term flooding is tolerated (Drapier, 1993b). It is very wind firm and rarely suffers from wind throw (Kausch-Blecken von Schmeling, 1994).

Silviculture for high-quality timber

Considering the growth characteristics of the wild service tree—a post-pioneer species with limited shade tolerance, a positive response to crown release, and a low tendency to produce epicormic shoots after high-intensity interventions (Lanier *et al.,* 1990; Bastien, 1997)—silviculture should be active, dynamic, and applied at the individual tree level. It is best compared to the management of other valuable broadleaved species, with the closest similarity to wild cherry (Lanier, 1986).

Wild service tree is most often planted in mixtures with other noble hardwood species such as oak, wild cherry, hornbeam, maple e.g., as it does not perform well in monocultural plantations (Sevrin, 1992). One year old seedlings grown in plant containers usually reach a height of 40–80 cm (Raguin and Boulet-Gercourt, 2000) and could be planted in groups of 2–3 individuals in a mixture with other broadleaves with a spacing of 1.5–2 metres.

Seedlings are prone to browsing by small mammals, rabbits and ungulates and should be protected by fence, or individual protective tubes or cages (Harper, 1981; Drapier, 1993b; Skovsgaard and Graversgaard, 2013c).

As with other pioneer species, reducing competing vegetation in the establishment phase is crucial to obtain satisfactory growth and stem quality (Crave, 1985; Drapier, 1993b; Gonin *et al.,* 2017). Soil preparation and a continuous high intensity weed control should be performed until seedlings have grown out of harm's way from competing ground vegetation, usually around 1.5–2 metres, depending on site conditions.

Continuous thinning interventions should be implemented with high intensity to keep the crowns free from competing vegetation, while still maintaining a lateral shading of the stem to encourage an upward growth and limiting the production of branches. Nursery trees with a slower initial growth such as hornbeam and field maple could be used for this (Drapier, 1993b; Wilhelm, 1993). Wild service trees seem to have a habit of ascendingly growing branches creating a "chandelier" formed crown (Crave, 1985; Drapier, 1993b; Wilhelm, 1993; Nicolescu *et al.,* 2009), this can cause forking and need to be maintained to produce high-quality timber.

Future crop trees should be selected and marked at an early stage, formative pruning of forks, as well as thick and ascending branches should be performed when necessary, preferably when trees are around two metres. High pruning up to at least 3 metres, ideally 6–7 metres, should then be performed to produce straight, knot-free, clean logs suitable for wood- and veneer products (Crave, 1985; Drapier, 1993b; Wilhelm, 1993; Gonin *et al.,* 2017). A breast height diameter of at least 60 cm should be reached in 100–120 years at suitable sites with an active and successful silviculture regime, however a rotation age of 50–70 years can be reached under optimal conditions (Bastien, 1997; Montero *et al.,* 2002).

Timber use

Wild service tree produces exceptional high-quality hardwood, often fetching premium prices on European markets. The timber is dense, fine-grained, and comparable to that of wild pear or cherry, with excellent properties for veneers, cabinetry, musical instruments, and luxury furniture (Skovsgaard and Graversgaard, 2013a; Werres, 2018). Its mechanical and aesthetic qualities, including a warm reddish hue and smooth texture, make it one of the most sought-after native hardwoods in central Europe. However, commercial use has remained limited due to its scattered distribution, low natural regeneration, and lack of targeted silvicultural practices (Lanier, 1990; Bastien, 1997). As interest in climate-resilient species grows, wild service tree is increasingly viewed as a promising option for high-value timber production, particularly in mixed-species stands or small-scale intensive forestry. Establishing well-performing seed sources and improving early stem form through formative pruning are essential to realizing its full economic potential.

2. Material and methods

The seed source trial was established in autumn of 2019 and replicated at three former agricultural sites. Establishment and the two first growing seasons are described in detail by Guest and Skovsgaard (2021). The most important parts are summarized.

Total height of the wild service trees, dieback on the apical shoot, and mortality were recorded after establishment and after each growing season (Guest and Skovsgaard, 2021). Additional field measurements for quality traits were collected in February 2023. A spring- and autumn phenology study was performed in 2023 at one of the sites.

Due to a fortunate delay, additional field measurements performed in April 2024 was added to the study. Total height, DBH, and occurrence of apical shoot dieback were recorded. Recording total number of branches and pruning half of the wild service trees in each plot were performed at all sites.

2.1 Establishment of the seed source trial

2.1.1 Seed sources and trial sites

The seeds were collected in autumn of 2018 from some of the best available wild service trees in forests and seed orchards in England, France, Germany, and Italy. In total, nine seed sources were included in the trial *(Table 1, Fig. 3)*.

Table 1. Seed source location and local site conditions. The naming of seed sources outside of England is by region, nearest town, or village. Name in italics indicates forest sites, name in standard font indicates seed orchard. Climate period 1991-2021 (ECMWF, 2024)

Seed source	Number of seed trees	Altitude (m)	Mean annual temperature °C	Mean annual precipitation (mm)
1 *Ast Wood, England*	6	85	10.1	735
2 *Stoopers Wood, England*	Ca. 12	95	10.2	749
3 *Tortoiseshell Wood, England*	5	110	9.9	716
4 Escatalens, France	Unknown	85	13.8	749
5 Harcourt, France	Unknown	130	10.8	776
6 Rahay, France	Unknown	130	11.8	735
7 *Lugny-Plottes Chardonnay, France*	Unknown	275	12	1120
8 *Sailershausen, Germany*	25–30	360	8.5	670
9 *Righi, Italy*	Unknown	280	12.9	1152
Mean		167	11	822

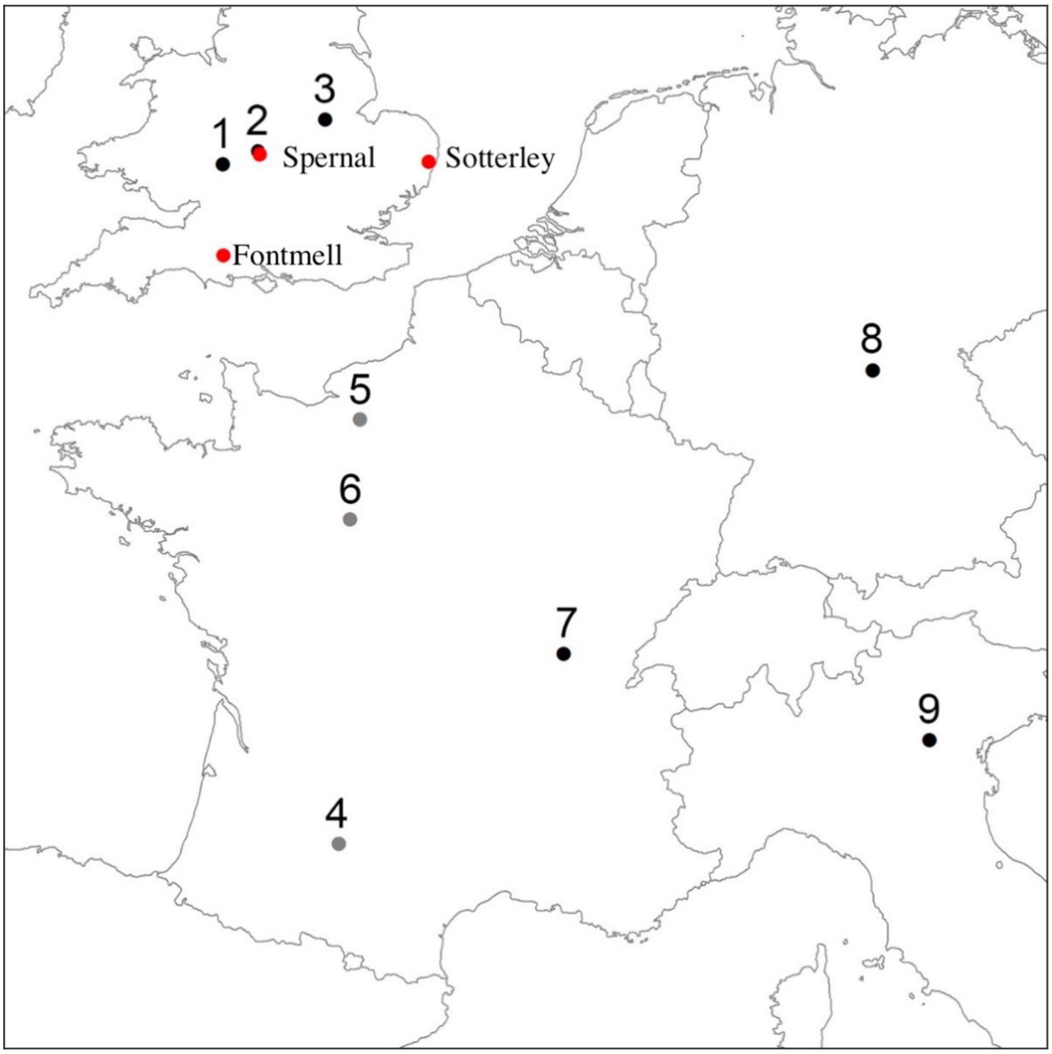

Figure 3. Location of seed sources and trial sites for the experiment. Legend: red = trial sites, black = forest site seed source, grey = seed orchard.

Table 2. Location and site details for the three trial sites. Coordinates are approximate and indicate the centre of each trial site

Site	Coordinates WGS 84	Altitude (m)	Slope	Temp§ °C	Precipitation§ mm
Fontmell	50.948458, -2.1866494	100	Northwest	8	900
Sotterley	52.401470, 1.5897265	20	South	7	620
Spernal	52.237656, -1.7742437	70	Flat	6	610

§: Approximate mean annual temperature and precipitation.

Ast Wood, 5 km west of Ledbury, Herefordshire, England
Seeds collected from six trees selected for their good stem form. The area is gently undulating, lying at elevations of around 100 to 200 meters above sea level. The region experiences a temperate maritime climate with mild, wet winters and warm summers, typical of western England. The soils are slightly acid, loamy, and clayey, with impeded drainage. These soils retain moisture well but can be prone to waterlogging in wet conditions. The fertility is moderate to high, providing favourable conditions for tree growth (LandIS, 2024).

Stoopers Wood, Warwickshire, England
Seeds collected from about 12 trees selected for their good stem form. Situated on slightly rolling terrain, with elevations ranging from 80 to 150 meters above sea level. The area has a temperate maritime climate, with moderate rainfall spread throughout the year, mild winters, and warm summers. Soils are slightly acid, loamy, and clayey, with moderate to high fertility. Impeded drainage is common, leading to periodic water saturation in wetter months. The fertility is moderate to high, providing favourable conditions for tree growth (LandIS, 2024).

Tortoiseshell Wood, 3.5 km northwest of Castle Bytham, Lincolnshire, England
Seeds collected from five trees selected for their good stem form. The area is relatively flat or gently sloping, lying at elevations between 50 and 100 meters above sea level. The area has a temperate maritime climate, with moderate rainfall spread throughout the year. Winters are cool, and summers are mild to warm, with lower annual precipitation compared to western England. Soils are slowly permeable, seasonally wet, and slightly acid but base rich. They are composed of loamy and clayey materials, providing moderate fertility. The seasonal wetness results from slow drainage, but the base-rich nature supports diverse plant communities and healthy tree growth (LandIS, 2024).

Escatalens, 60 km north of Toulouse, France
"A 20-year-old trial and seed orchard with a collection of fine wild service trees from throughout France", as described by Vilmorin, seed merchant, France (Vilmorin, e-mail, 20 September 2018). No further information was found, detailed origin and number of seed trees unknown.

As mentioned in literature review; a study on chloroplast DNA (Demesure *et al.,* 2000) showed very little differentiation and geographical structuring of the species in Europe. As a result, two regions of origin were defined based on ecological and climatic data, the north of France (STO901-Northern France) and the south-west and the Mediterranean region (STO902-Southern France) (Planfor, 2013; Muratorio, 2024). Even though the Escatalens seed orchard is in the south-west region, all French seed sources in the trial are likely classified as STO901.

Harcourt, 40 km southwest of Rouen, Normandy, France

An arboretum and seed orchard that supplies Vilmorin with wild service tree seeds (Vilmorin, e-mail, 20 September 2018; Drège, 2022). Detailed origin and number of seed trees unknown.

Rahay, 70 km east of Le Mans, Pays de la Loire, France

A quite young seed orchard (about 15 years) with mixed origin from France. The parent trees were selected and established by Centre Régional de la Propriété Forestière (CRPF, French forestry organization for private forest owners) (Vilmorin, e-mail, 20 September 2018). Detailed origin and number of seed trees unknown.

Forests of Lugny, Plottes, and Chardonnay (L-P-C), 100 km south of Dijon, Burgundy, France

Seeds collected by the Office National des Forêts (ONF) from an unknown number of trees across three forests around Lugny, Plottes, and Chardonnay. The region is characterized by gently rolling hills, with elevations ranging between 200 and 400 meters above sea level. Burgundy experiences a temperate oceanic climate with continental influences, characterized by warm summers and cool, damp winters. Precipitation is evenly distributed throughout the year, though summer droughts are becoming more common due to climate change. Although the exact locations of the stands are unknown, the region is renowned for its complex soils and terroir, primarily associated with viticulture. The soils in Burgundy are predominantly limestone and clay, with varying proportions of marl, gravel, and sand, depending on local topography and geological formations (Sols de Bourgogne, 2024). These calcareous soils are well-drained and alkaline, promoting the growth of plant species adapted to such conditions.

Sailershausen, 25 km east of Schweinfurt, Northern Franconia, Germany

One of the most well-known and documented origins of wild service tree, located in the Sailershausen University Forest, owned and managed by Würzburg University. The forest holds many magnificent wild service trees with a majority growing on warm hillsides with limestone soil on the upper Muschelkalk. All trees are marked, numbered and measured every five years, in total there are around 1 500 individuals and a handful are harvested each year. Sailershausen was one of the best ranked provenances in the provenance trial in Lilliental established in 1979 along with Schweinfurt, and Würzburg which all grow in the same region (Skovsgaard and Graversgaard, 2013a). The seeds from these provenances are therefore desired by plant nurseries and foresters. Seed collected from 25-30 trees distributed across three parts of the forest covering approximately 100 ha.

Righi, Perarolo, Arcugnano, Veneto, 60 km east of Venice, Italy

Provided by Vilmorin, unknown number of seed trees collected in a forest outside the village of Perarolo, Arcugnano – seed source number 134 in the regional register of certified forest seed sources in the Veneto region. The area is characterized by hilly terrain with elevations ranging from approximately 100 to 400 meters above sea level. The area experiences a humid subtropical climate, with warm summers and cool, damp winters. The soil is primarily calcareous, derived from limestone bedrock, which contributes to a well-drained and alkaline environment (Lasen and Wilhalm, 2001). Due to a misunderstanding, in the previous report from 2021, this was thought to be another seed source from Parco Cavaioni, just south of Bologna.

Table 3. Seed source locations, collection, and sowing date. WGS coordinates indicate exact (italics) or approximate location (standard font)

Seed Source	Coordinates WGS 84	Date Seed Collected	Received by Forestart	Seed viability 11 Feb 2019	Sowing Date
1 Ast Wood	*52.043180, -2.479185*	Oct -18	8-nov-18	80%	End-Mar-19
2 Stoopers Wood	*52.268200, -1.822795*	Oct -18	8-nov-18	70%	End-Mar-19
3 Tortoiseshell Wood	*52.768940, -0.574760*	21-Oct-18	8-nov-18	80%	End-Mar-19
4 Escatalens	*43.968020, 1.186480*	-	24-Jan-19§	40%	5-Jun-19
5 Harcourt	*49.174440, 0.791125*	Nov-18	24-jan-19	40%	5-Jun-19
6 Rahay	*47.940600, 0.816400*	-	24-jan-19	60%	5-Jun-19
7 L-P-C	46.503180, 4.842420	Nov-18	7-feb-19	90%	5-Jun-19
8 Sailershausen	50.060000, 10.450585	Oct -18	14-nov-18	40%	End-Mar-19
9 Righi	45.472096, 11.489772	Nov-18	24-jan-19	90%	5-Jun-19

§: dirty seeds

Plant propagation and grading of planting stock

The professional seed merchant Forestart propagated all the seed sources at local facilities, ensuring similar treatment throughout the stratification process, and maximising germination success. Stratification was performed by cold treatment (3°C) for three months, 900 seeds from each seed source were then sown into growing containers. Ast Wood, Stoopers Wood, Tortoiseshell Wood and Sailershausen were received in November 2018. After stratification, these seeds were sown at the end of March 2019. Due to a delay in delivery, the seeds from Escatalens, Harcourt, Rahay, Lugny-Plottes-Chardonnay (L-P-C), and Righi did not arrive until late January, stratification could only commence in February with seeds ready for sowing on the 5th of June 2019.

The growth progress was assessed on July 16th, 2019, and it was evident that the seed sources sown in March would generate strong straight 40–60 cm tall saplings ready for planting in November 2019. For the seed sources sown in June, major differences in germination success were visible. These seed sources (except for L-P-C) showed signs of low seed viability, possibly due to the late arrival of the seeds.

Given the germination success of all the wild service tree seed sources, through selection and grading out, a total of 216 saplings (72 saplings per site, including 8 spare saplings to replace any damaged or dead saplings) of the tallest, best quality wild service saplings, per seed source were used in the trial. A size class of 40-80 cm was achieved for the following seed sources: 1. Ast Wood, 2. Stoopers Wood, 3. Tortoiseshell Wood and 8. Sailershausen. These are the English and German seed sources, which were sown by the end of March.

The second group of seed sources, the French and Italian, were generally shorter than those in the first group, as they were not sown until the 15th of June 2019. The seed source Lugny-Plottes-Chardonnay clearly produced the tallest saplings from these. Generally, a size class of 20-40 cm was achieved for the second group of seed sources.

Figure 4. All nine seed sources in Forestart's nursery, 16 July 2019. Note the difference in size and germination rate. Photo: Christopher Guest

Figure 5. High quality Sailershausen sapling, 16 July 2019. Photo: Christopher Guest

Site soil characteristics

The soil characteristics were analysed in 1-metre-deep soil pits. The following were recorded at each soil pit: depth of plough layer, horizons present and corresponding depths, presence of free lime within each horizon, presence of reduction/mottling in B and C horizons and depth at which any groundwater occurs. Soil samples were taken by removing an equal amount of soil through the complete profile irrespective of the depth of the individual horizons. Each soil sample consisted of approximately 500 grams of soil.

Each soil sample was subsequently analysed in a laboratory for the following chemical characteristics and elements: pH, C, N, P, K, Ca, Mg (and other micronutrients), organic content and soil texture.

All soils at Fontmell, Sotterley and Spernal had distinct 30 cm plough layers. The soils at Fontmell were all well aerated while the soils at Sotterley and Spernal showed mottling and reduction in the B and C horizons which are characteristic of surface water gleysols.

Table 4. Summary of soil characteristics for blocks 1-4 (mean values for depth = 0-100 cm) at each site at the time of planting. C/N = carbon/nitrogen ratio, CEC = cation exchange capacity, BS = base saturation (percentage of potential CEC occupied by Ca, Mg, K and Na cations). More detailed soil data can be found in Appendix 1

Site	Fontmell	Sotterley	Spernal
Terrain	Northwest-facing slope	South-facing slope	Flat
Soil type	Calcareous brown earth	Surface water gley	Surface water gley
Org. matter (%)	2.5	1.2	2.4
Sand (50 - 2000 µm, %)	50	40	33
Silt (5.69 - 50 µm, %)	28	27	36
Clay (0 - 5.69 µm, %)	22	33	31
pH	8.0	7.9	8.2
C/N	11.0	11.5	12.6
CEC (meq/100g)	14.5	17	26.5

Site preparation and maintenance

The Fontmell site had been set aside for one year before preparation, it was formerly used for pasture and as a wheat field. Prior to cultivation, the site was sprayed with glyphosate to reduce competing vegetation. The site was then shallow ploughed (in very wet conditions), and triticale (variety Fido) was sown in November 2019 at 86.45 kg/ha as a cost-effective and environmentally friendly weed control. The triticale germinated well and established uniformly across the site. Planting was carried out in mid to end of November 2019. The site was fenced, and protective tubes (Tubex) were put around WST and the field maple.

The triticale kept competing vegetation low in the first season and only occasional removal of weeds were carried out in summer 2021. Due to high local rodent activity, the regeneration of triticale was compromised. Early June 2022 small vulnerable seedlings were released and the rows between the seedlings were mowed in late June 2022, followed by trampling around smaller seedlings in August. In late June 2023 the rows between the seedlings were mowed in one direction up and down the slope, followed by trampling around the seedlings.

The site at Sotterley was used as a horse paddock until recently and 10 years prior to this it was a good wheat field. Prior to cultivation the site was sprayed with glyphosate to reduce competing vegetation, it was then mole drained and sub-soiled. Due to a very wet October in 2019, the triticale failed to successfully germinate and establish due to the seed not being drilled, combined with poor weather and damage by slugs. Planting was carried out in mid to end of November 2019. The site was fenced, and protective tubes (Tubex) were put around the wild service trees.

Even though the triticale was not established, the competing vegetation was not of major concern at this site. Mowing was performed between the planting lines in both directions in August 2021 and early June 2022. Straw mulch mats were placed around each wild service tree sapling to retain water, which also reduced competing vegetation. In late June 2023 the rows between the trees were mowed in both directions.

The agricultural site at Spernal was left fallow for one year prior to establishment of the trial, before this it was a wheat field. All land owned by the Heart of England Forest is managed organically, therefore the triticale was sown in October 2019 by direct drilling into the vegetation already present, mainly volunteer wheat and arable weed grasses. Due to extremely wet conditions in October 2019 (the field was under water for a period), the seeds failed to germinate, and no triticale was established. Planting was carried out at the end of January 2020. The site was fenced, and protective tubes (Tubex) were put around the wild service trees.

Competing vegetation was of most concern at the Spernal site. Manual weeding and trampling were carried out around each wild service tree sapling in late May 2020 combined with irrigation. In October 2020 the planting lines were mowed in both directions to make saplings more visible for a beating-up assessment. The same type of mowing was repeated in early August 2021. In 2022 the site was mowed in early June, followed up by trampling around seedlings in the end of July. In May 2023 the site was mowed in one direction followed by trampling of grass around the admixed species in August and September.

Figure 6. Successful germination of triticale at Fontmell, April 2020. WST and field maple in protective tubes. Photo: Christopher Guest.

2.1.2 Species mixture and statistical design

Considering the common forest type in which wild service tree is found in central Europe (Rodwell, 1991; Wohlgemuth, 1993; Pleines, 1994) and given the general and possibly increasing risk associated with the planting of pure stands, the wild service trees were planted in a mixture with field maple (*Acer campestre* L.*)*, European hornbeam (*Carpinus betulus* L.*)* and pedunculate oak (*Quercus robur* L.*)*. Extraction racks were planted with common hazel (*Corylus avellana* L.). Early seed setting may give hazel the opportunity to spread across the area as an understorey species.

This mixture mimics a forest type that prevails in some parts of the natural range of wild service tree. By planting the trial as a mixture, the growth depression and health problems that sometimes seem to occur in pure stands of *Rosaceae* species may be prevented (Coello *et al.,* 2013; Loewe *et al.,* 2020).

The trial was established as a randomised complete block design. Each wild service tree seed source was planted in a group pattern (4 × 4 saplings per seed source), with one group of each seed source per block *(Fig. 7)*. A total of 4 blocks were planted on each site (576 wild service trees in total per site).

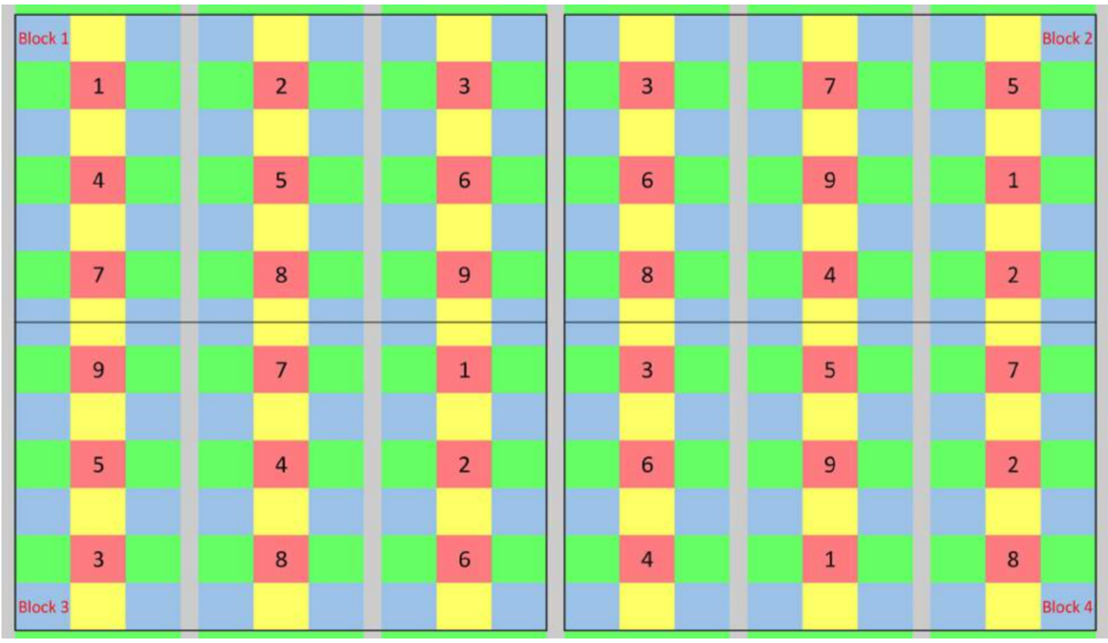

Figure 7. Block layout at site level (blocks 1-4), including parts of the buffer zone. Legend: red = wild service tree, green = oak, blue = hornbeam, yellow = field maple, grey = hazel. Note the different (randomized) location of seed sources in the blocks. Net block size: 39 m x 58 m (2262 m2).

All species were planted at a spacing of 1.5 m × 1.5 m except extraction racks which were planted with common hazel at a spacing of 2.0 m x 2.0 m, i.e. hazel planted 2.0 m from the neighbouring lines of saplings to the left and right and 2.0 m between hazel saplings within this line.

Each site was planted with an external buffer zone consisting of 4 rows of pedunculate oak also planted at a spacing of 1.5 m x 1.5 m, except where extraction racks were continued on from the trial with hazel at a spacing of 2.0 m x 2.0 m. Permanent extraction racks were laid out at establishment to allow good access for harvesting machinery, limit ground compaction and avoid the need to drive any machinery near the groups of wild service tree.

2.2 Data collection

2.2.1 Survival, total height, and apical shoot dieback

In addition to initial measurements of survival, total height, and the occurrence of apical shoot dieback recorded in 2019-2021 (Guest and Skovsgaard, 2021), further data collection was performed in February 2023, assessing growth and quality traits for the third growing season. In April 2024, total height and occurrence of apical shoot dieback were measured for the fourth growing season after planting.

The heights of all wild service saplings were measured after establishment in 2019 to attain the initial starting height. After each growing season, total height of all wild service trees was recorded in centimetres. In conjunction with height measurements, apical shoot dieback and shoot snap-off was recorded. Mortality was recorded, dead saplings were replaced in December of 2020 and 2021, and the initial height for the replacement sapling was recorded.

2.2.2 Forking height and forking angle

Forking height was recorded in centimetres, if a seedling had multiple forks, height for the first fork from the ground was recorded. The height was recorded at the base of the fork. The angle of the fork was recorded in degrees using a digital protractor. Forking angles were not collected at Spernal.

2.2.3 Diameter at breast height and diameter of thickest branch

The diameter at breast height was recorded in millimetres for trees with height >130 cm. Diameter of the thickest branch (horizontal) was recorded for all trees in millimetres in February 2023. Data was not collected at the Spernal site as a large proportion of the seedlings were below 130 cm. In April 2024 diameter at breast height were measured at all sites.

2.2.4 Stem form and future crop tree

The stem form of all trees was evaluated independently of growth on a scale of 0-2.5 (0, 0.5, 1, 1.5, 2, 2.5); stem straight in 0, 1 or 2 planes, or intermediate between these (0.5 and 1.5). Score 2.5 was used for stems with score 0 or 0.5 at the base/in the tube and score 2 above the tube.

A general visual assessment of overall quality and vitality was made using a three-level scale to grade potential future crop trees. Grading performed before pruning.

1. Excellent form – Outstanding form and vitality with a straight stem, fine branching, and clear apical dominance.
2. Good form – Good overall form and vitality with apical dominance and no major stem defects
3. Poor form – Multiple stem defects such as low forking, twisted or swept stem, heavy branching.

2.2.5 Branch angles and branch type

Branch angles for the five most significant branches (generally the five largest branches by branch diameter) were measured for branch angle, counting the branches from the top of the tree; a fork counted as a branch and the branch angle of the fork was always noted as the first branch. Measurements were performed using a digital protractor measuring the angle between the stem and the start of the branch.

A visual assessment was made of the branch type with two different types; Normal= branches with a "normal" growth habit and Ascending= one or more significantly ascending branches present at the time of observation.

2.2.6 Number of branches and pruning

Half of the trees at Fontmell and Sotterley were pruned, the trees at Spernal were too small in 2023 as a majority had not grown out of the protective tubes (60 cm). The total number of branches, number of branches pruned, and the type of pruning were recorded. In April 2024, the total number of branches and pruning were recorded and performed at all sites.

A split-plot design was imposed on each WST plot, pruning half of the trees in each plot (8 of 16 trees). The direction of the split was randomized by block (i.e., the direction of the split was identical for all plots within each block).

Block 1	**N** (trees in the northern half were pruned, i.e. pos. 9-16; trees in the southern half were left un-pruned).
Block 2	**E** (eastern half, pos. 3, 4, 7, 8, 11, 12, 15, 16 were pruned).
Block 3	**S** (southern half, pos. 1-8 were pruned).
Block 4	**W** (western half, pos. 1, 2, 5, 6, 9, 10, 13, 14 were pruned).

Pruning types; 1 = Scattered in crown, 2 = Only fork pruned, 3 = Fork pruned, and one or more additional branches pruned, 4 = singling of double stem, 5 = singling of double stem and one or more additional branches pruned.

2.2.7 Additional notes

Additional notes such as damage, pests, and multi-tops or double stems were recorded.

2.2.8 Admixed species

All trees in the two central rows of the admixed species were recorded as alive or dead, original, or beaten-up, and were measured for total tree height in centimetres in February 2023, after the third growing season.

2.2.9 Spring and autumn phenology

A study of the spring and autumn phenology was performed at Spernal in 2023. Photos were taken once a week on eight occasions from April 13^{th} – June 1^{st} covering the leaf flush stage of the different seed sources. The leaf flush was graded using a 10-grade photographic scale (Appendix 2). The length of the apical shoot was measured in millimetres each week. The largest trees from each plot were selected as well as the furthest developed tree during the first week, sometimes being the same tree. In total 69 trees were studied.

Autumn phenology was performed in the same manner, photos taken each week on eleven occasions from 21^{st} of September – December 1^{st} were visually graded on a self-compiled 10-degree scale (Appendix 3) following the dormancy process. The same trees were analysed except that additional trees were added in the plots where only one tree was observed in the spring study. In total 72 trees were studied.

During data collection in April 2024, photos were taken of each plot at each site and a visual assessment grading of the spring flush was performed based on the photographs.

2.3 Data analysis

Statistical analyses were performed using RStudio (version 2024.12.1+563). Analyses were structured around growth- and quality-related traits and were applied to the remaining original population *(n = 1624)* and in some cases a Top 5 subset *(n = 540),* comprising the five tallest trees (without apical shoot dieback or negative height increment) per plot.

Growth-related analyses

Descriptive statistics were used to summarise tree height, height increment, diameter at breast height (DBH), and diameter of the thickest branch (DTB) across seed sources and sites. One-way analysis of variance (ANOVA) was used to assess differences in height, DBH, and DTB, with Tukey's honest significant difference (HSD) test applied for post-hoc comparisons. Levene's test for homogeneity of variance and the coefficient of variation (CV) were used to assess within-group variability.

To further explore the influence of genetic and environmental factors on annual height increment, a linear mixed-effects model (LMM) was fitted using restricted maximum likelihood (REML) estimation. Fixed effects included seed source, initial planting height, water availability (precipitation and irrigation), and soil properties (cation exchange capacity and carbon-to-nitrogen ratio), along with relevant interaction terms.

Model Structure

$$IH_ijt = \beta_0 + \beta_1(SS) + \beta_2(Hstart_j) + \beta_3(SS_i \times Hstart_j) + \beta_4(W5_t) + \beta_5(CEC_j) + \beta_6(W5_t \times CEC_j) + \beta_7(CNratio_j) + \beta_8(W5_t \times CNratio_j) + u_j + \epsilon_ijt$$

IH_{ijt} = Height increment of tree *j* from seed source *i* in year *t*

β_0 = Intercept

$\beta_1 SS_i$ = Fixed effect of seed source

$\beta_2 Hstart_j$ = Fixed effect of initial height

$\beta_3(SS_i \times Hstart_j)$ = Interaction between seed source and initial height

$\beta_4 W5_t$ = Fixed effect of water availability (precipitation & irrigation)

$\beta_5 CEC_j$ = Fixed effect of soil cation exchange capacity

$\beta_6(W5_t \times CEC_j)$ = Interaction between water availability and soil CEC

$\beta_7 CNratio_j$ = Fixed effect of soil carbon-to-nitrogen ratio

$\beta_8(W5_t \times CNratio_j)$ = Interaction between water availability and CN ratio

u_j = Random intercept for each tree (accounting for individual variation)

ϵ_{ijt} = Residual error

A random intercept was included for individual trees to account for repeated measures. In addition, Pearson correlation analysis was used to examine the relationship between initial seedling height and subsequent height growth.

Quality-related analyses

Variation in stem form was analysed using descriptive statistics, two-way ANOVA, and Levene's test. A linear mixed-effects model was also fitted to evaluate the effects of seed source, site, and total height increment, with block and seed source structure included as random effects. Least square means (LS means) were calculated to adjust for height-related variation and facilitate comparison between seed sources. A random intercept was included for each tree (u_j) to account for individual variation in growth. This helps control for unmeasured differences between trees, such as genetic variation or microenvironmental factors.

Model structure

$$SF_{ijk} = \beta_0 + \beta_1(Site_i) + \beta_2(SS_j) + \beta_3(Site_i \times SS_j) + \beta_4(IHTotal) + (1|Block{:}Site) + (1|Site{:}Block{:}SS) + \epsilon_{ijk}$$

SF_{ijk} = stem form rating for an individual tree

β_0 = intercept

$\beta_1(Site_i)$ = effect of site

$\beta_2(SS_j)$ = effect of seed source

$\beta_3(Site_i \times SS_j)$ = interaction between site and seed source

$\beta_4(IHTotal)$ = effect of total height increment as a covariate

$(1|Block{:}Site)$= random effect of block within site

$(1|Site{:}Block{:}SS)$ = nested random effect of seed source within block and site

ϵ_{ijk} = residual error

Mean branch angle was analysed using a similar LMM structure. The model accounted for seed source, site, their interaction, and total height increment, with block and nested seed source structure as random effects. Variance partitioning was conducted to estimate the relative contributions of genetic, environmental, and micro-site variation.

Model structure

$$BA_ijk = \beta_0 + \beta_1(Site_i) + \beta_2(SS_j) + \beta_3(Site_i \times SS_j) + \beta_4(IHTotal) + (1|Block{:}Site) + (1|Site{:}Block{:}SS) + \epsilon_ijk$$

BA_{ijk} = branch angle measurement for tree *k* at site *i* and seed source *j*

β_0 = intercept

$\beta_1(Site)$ = fixed effect of site

$\beta_2(SS)$ = fixed effect of seed source

$\beta_3(Site \times SS)$ = interaction effect between site and seed source

$\beta_4(IHTotal)$ = total height increment as a covariate

(1 |Block:Site) = random effect of block within site

(1 |Site:Block:SS) = random effect of seed source within block and site

ϵ_{ijk} = residual error

Branch type (normal vs. ascending) was analysed as a categorical variable using Pearson's Chi-squared test to assess its association with seed source and site combinations. Apical shoot dieback and forking were similarly tested using a contingency table and Chi-squared analysis. Future crop tree classification was evaluated with a two-way ANOVA to assess the effects of seed source, site, and their interaction on classification outcomes.

2.4 Precipitation and irrigation

2.4.1 First growing season – 2020

Local data was available at Fontmell and Sotterley. At Spernal, a NextGen water site, 2 km north of Spernal Estate was used for precipitation data. In the late spring and summer of 2020, conditions became very dry and during May almost no rainfall was recorded at any of the sites. In the end of May the decision was made to irrigate the wild service trees, at Fontmell the field maple was irrigated as well.

Table 5. Precipitation data per month for 2020 (mm)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Fontmell	93	152	63	57	4	82	38	116	55	171	79	146	1056
Sotterley	40	89	30	22	3	60	42	37	118	89	30	111	671
Spernal	46	120	23	28	2	85	63	115	35	130	48	111	806

In April-August Fontmell received 295 mm of natural downfall, with 116 mm (39 %) falling in August. The wild service trees and field maple were watered once with approximately 9 litres per sapling.

At Sotterley 165 mm fell during the same period with 37 mm (23 %) in August. Here the ground in between the planting lines was rotovated after the first watering to improve the water absorption capability due to the large cracks present during the drought. The saplings did not have much protection as the triticale had failed to establish and weed growth was also very limited due to the drought.

Spernal received 295 mm with 115 mm (30 %) in August. Hence, the natural downfall was quite similar at Fontmell and Spernal, while Sotterley received approximately half as much natural precipitation. Adding the estimated volumes of irrigated water to May and June, the seedlings at Fontmell received 95 mm, Sotterley 91 mm and Spernal 247 mm during these two months.

Table 6. Estimated volume of irrigated water in 2020 (litres per seedling ≈ mm per square meter)

Date	Fontmell	Sotterley	Spernal
24 May		3.8	
26 May		6.1	40
27–28 May	9		
29 May		6.1	30
1 June		6.1	
2 June			30
5 June		6.1	
11 June			30
25 June			30
Total	9	28.2	160

2.4.2 Second growing season – 2021

The second growing season started off rather dry as very little rainfall was recorded in April. However, all sites received sufficient downfall during the following summer months, and no irrigation was implemented this year. Data from the NextGen site close to Spernal was not available, so data from the meteorological station in Oxford, 65 km southeast of the trial, was used as a proxy. In 2020, Oxford received 1 % more than the NextGen site (i.e., rainfall at Oxford was nearly identical). It can be estimated that the Spernal site received about 291 mm during April-August 2021. Fontmell received a similar amount of rainfall during the growing season (297 mm) while Sotterley received slightly less (241 mm). The main difference in the precipitation pattern during the growing season was the very limited rainfall in April (during leaf flush) at Fontmell (9 mm) and Sotterley (5 mm) compared to Spernal (27 mm).

Table 7. Precipitation data per month for 2021 (mm)

Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Fontmell	106	71	42	9	99	49	110	31	38	172	14	89	830
Sotterley	92	48	31	5	81	78	55	22	24	94	35	72	637
Spernal§	55	55	30	27	95	68	68	35	44	92	18	67	654

§: Oxford representing Spernal precipitation

2.4.3 Third growing season – 2022

The third growing season presented a dry winter and spring, with limited downfall in April. Sotterley experienced a particularly dry spring and summer, with 98 mm recorded during the growing season (April-August), causing mature trees to shed leaves in July due to drought conditions. Sotterley had a total precipitation of 504 mm compared to the long-term average of 624 mm. Had November been an average rainfall month of 64 mm, 2022 would have been a record dry year of 424.2 mm, beating 2011 where 429.2 mm was recorded. However, Sotterley received more than double the average in November with 145 mm rainfall recorded.

Spernal also experienced a very dry July and August with 104 mm recorded during the growing season (April-August) at the Oxford station. At Fontmell, July was a dry month as well with only 6 mm recorded, although with a higher precipitation in August with a total rainfall of 135 mm during the growing season (April-August).

Table 8. Precipitation data per month for 2022 (mm)

Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Fontmell	34	65	73	24	42	34	6	29	84	163	184	130	868
Sotterley	19	66	22	6	40	43	3.3	5	45	63	145	47	501
Spernal[§]	20	63	41	14	42	50	7	4	55	79	107	67	549

§: Oxford representing Spernal precipitation

As a result of the very dry conditions, it was decided to irrigate the wild service trees again, starting with Sotterley at the end of June. The seedlings received a total of 60.56 litres spread over four times at Sotterley; fresh barley straw was laid out in June around each wild service tree at Sotterley to aid the retention of moisture. At Spernal mulch mats were added around the wild service trees to supress weed growth. Fontmell and Spernal were irrigated once with approximately 18 litres per seedling. At Fontmell and Spernal the first two lines of admixed species around each wild service tree group were irrigated as well.

Table 9. Estimated volume of irrigated water in 2022 (litres per seedling ≈ mm per square meter)

Date	Fontmell	Sotterley	Spernal
27 June		15.14	
25 July		15.14	
10 August		15.14	
25 August		15.14	
3-11 August	18		
5-19 August			18
Total	18	60.56	18

2.4.4 Fourth growing season – 2023

The fourth year was the wettest at all sites since establishment and the second wettest at Sotterley since measurements started in 1956, only exceeded in 2001 when 852 mm were recorded. Although February being record dry, the precipitation during April-August was more than the double at all sites compared to previous year, with 363 mm recorded at Fontmell, 265 mm at Sotterley, and 324 mm at Spernal.

Table 10. Precipitation data per month for 2023 (mm)

Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Fontmell	110	12	119	79	55	34	131	64	72	149	119	171	1115
Sotterley	54	4	73	51	75	21	118	53	91	147	86	72	845
Spernal[§]	57	8	134	66	51	42	100	65	73	138	79	117	930

§: Oxford representing Spernal precipitation

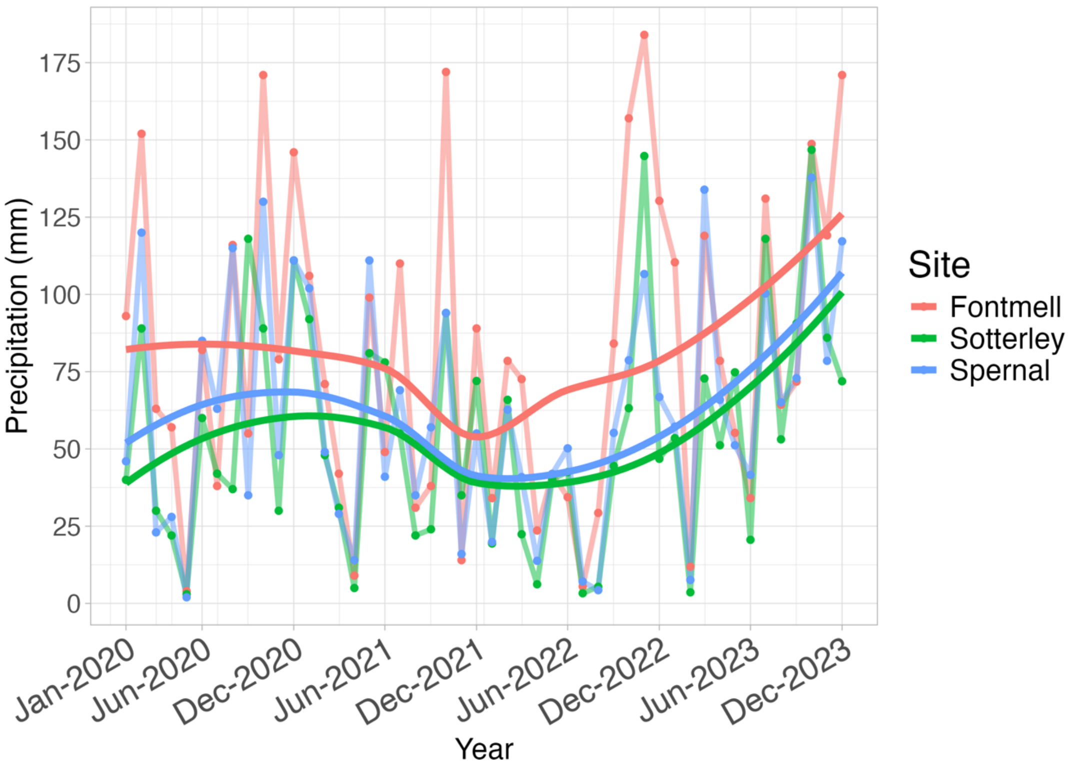

Figure 8. Monthly precipitation at all three sites during 2020-2023 with regression trend lines.

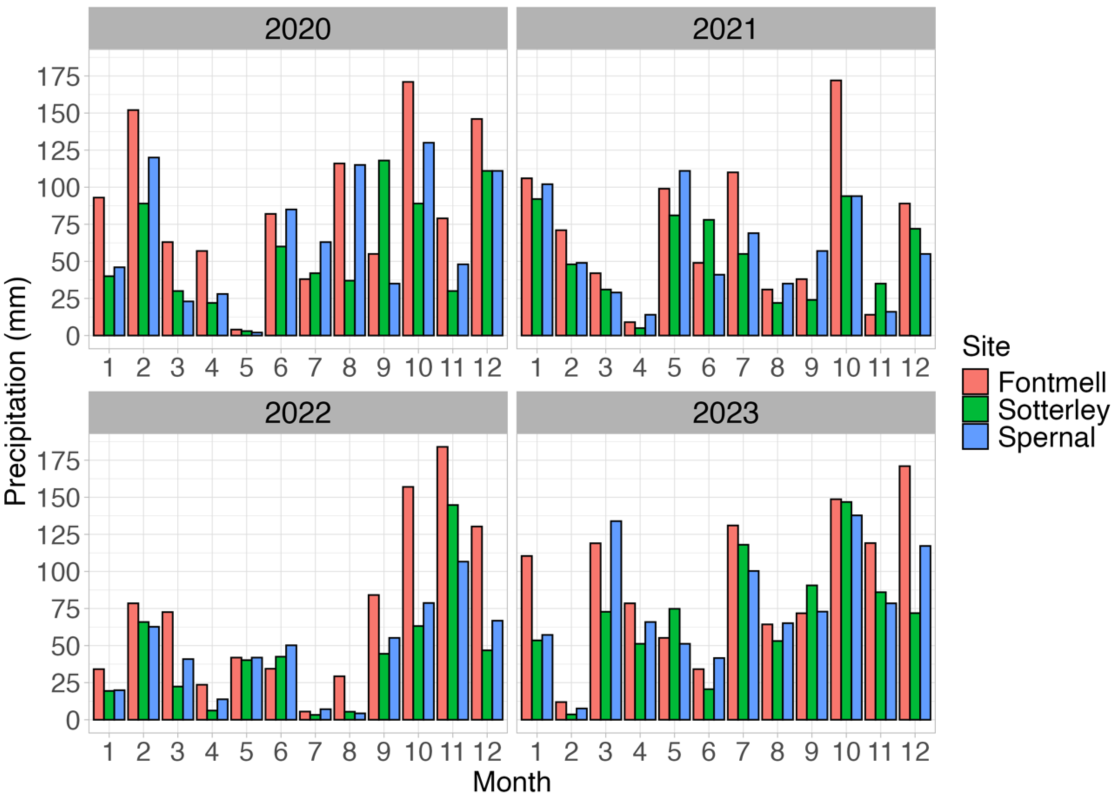

Figure 9. Monthly precipitation at all three sites during 2020-2023.

3. Results

3.1 Survival and health

First growing season – 2020

The Fontmell site had the highest survival rate at 99 % with just six dead saplings, which could be attributed to the successful establishment of triticale and higher precipitation in March and April. The drought in early spring and more competing ground vegetation caused a higher mortality at Sotterley (43) and Spernal (49), which had a similar survival at 92.5 % and 93.5 % after the first growing season. Significant losses of the admixed species were recorded at Sotterley and Spernal, at Fontmell almost no mortality was recorded.

Table 11. Mortality the first two growing seasons and total survival rate. n=remaining saplings of original population after the first two growing seasons (64)

Site	Fontmell				Sotterley				Spernal			
Seed source	Mor. 2020	Mor. 2021	n	Surv. rate %	Mor. 2020	Mor. 2021	n	Surv. rate %	Mor. 2020	Mor. 2021	n	Surv. rate %
1 Ast Wood	0	0	64	100	4	0	60	93.8	4	0	60	93.8
2 Stoopers Wood	3	0	61	95.3	7	0	57	89.1	3	0	61	95.3
3 Tortoiseshell Wood	2	0	62	96.9	1	0	63	98.4	2	0	62	96.9
4 Escatalens	0	0	64	100	7	2	55	85.9	9	0	55	85.9
5 Harcourt	0	0	64	100	7	0	57	89.1	5	0	59	92.2
6 Rahay	0	0	64	100	2	0	62	96.9	10	1	53	82.8
7 L-P-C	0	0	64	100	5	0	59	92.2	3	1	60	93.8
8 Sailershausen	1	1	62	96.9	5	0	59	92.2	3	0	61	95.3
9 Righi	0	0	64	100	5	0	59	92.2	10	1	53	82.8
Total	6	1	569	98.8	43	2	531	92.2	49	3	524	91

Second growing season – 2021

The higher precipitation in the spring and summer months was visible in both survival rate and growth throughout all sites. The total mortality at Fontmell was one wild service tree, two at Sotterley (four if beat-ups were to be added) and three at Spernal (seven with beat-ups from last year). The admixed species suffered significant losses at Sotterley and Spernal this growing season as well, almost no losses were recorded at Fontmell.

Third growing season – 2022

Despite limited precipitation at the start of the year followed by a hot and dry growing season, no mortality of wild service tree was noted, and all seed sources across all sites where performing better. However, without the irrigation some seedlings would likely have succumbed to the drought and the growth rates would have been lower. The admixed species were also doing better during the third growing season, with a higher survival rate at Sotterley and Spernal, and with almost no mortality at Fontmell.

Fourth growing season – 2023

The higher precipitation and further developed root systems was portrayed in survival and height increment at all sites, no mortality was recorded. Sotterley had the best performing wild service trees with the highest total mean height, and mean height increment. Righi at Fontmell had the highest mean height increment, at 52 centimetres. The Spernal site had significantly higher growth rates this year with many seed sources performing twice as good compared to earlier years.

The three best performing individuals this year were all found at Sotterley. Notably, a Rahay tree grew from 74 cm to 245 cm, showcasing an impressive growth of 171 cm in one growing season. The second highest increment was by a Righi tree that grew from 155 cm to 279 cm, an increment of 124 cm. The third best individual was a Harcourt tree that grew from 134 cm to 257 cm, an increment of 123 cm.

Table 12. Summary of fourth-year measurements (mean values per site and seed source; original population). Legend: H_3 = height at the end of the third growing season (2022). n = Total number of seedlings from original population (64). H_4 = height at the end of the fourth growing season (2023). I_{H4} = Fourth-year growth. Data after first year based on original population, disregarding beat-ups

	Fontmell				Sotterley				Spernal			
Seed source	H_3 cm	n	H_4 cm	I_{H4} cm/y	H_3 cm	n	H_4 cm	I_{H4} cm/y	H_3 cm	n	H_4 cm	I_{H4} cm/y
1 Ast Wood	104.2	64	131.1	26.9	126.5	60	162.9	36.4	90.1	60	118.4	28.3
2 Stoopers Wood	106.7	61	139	32.3	129	57	172.7	43.7	95.2	61	124.1	28.9
3 Tortoiseshell Wood	117.3	62	156.2	38.9	125.5	63	164.7	39.2	91.5	62	120.8	29.3
4 Escatalens	115.8	64	160	44.2	120.9	55	163	42.1	76.6	55	111.1	34.5
5 Harcourt	111.7	64	149.5	37.8	132.6	57	175.2	42.6	80.1	59	114.6	34.5
6 Rahay	128.2	64	170.6	42.4	142.4	62	188.3	46	86.4	53	120.5	34.1
7 L-P-C	131.7	64	175.9	44.2	150.4	59	188.2	37.9	105.3	60	143.4	38.1
8 Sailershausen	116.1	62	155.7	39.6	132.5	59	180.8	48.3	100.4	61	132.7	32.3
9 Righi	130.1	64	182.1	52	150.9	59	198.3	47.4	90.2	53	132	41.8
Total	118	569	157.8	39.8	134.5	531	177.1	42.6	90.6	524	124.2	33.5

§: Lugny-Plottes-Chardonnay

The three best performing individuals after all four growing seasons were the Rahay tree mentioned above that grew from 26 cm to 245 cm with a total height increment of 222 cm. The Harcourt tree also mentioned above, that grew from 42 cm to 257 cm with a total height increment of 197 cm. The third best individual was a Righi tree at Fontmell that grew from 36 cm to 251 cm, with a total height increment of 191 cm.

3.1.1 Admixed species

The admixed species suffered heavy losses during the first three growing seasons at Sotterley and Spernal due to the very hot and dry weather conditions *(Table 13)*. However, a steady annual decrease in mortality was seen for all admixed species, except for oak at Sotterley after the second growing season. The field maple seemed to cope best with the dry conditions out of the admixed species at Sotterley and Spernal. Although, the field maple at Fontmell was irrigated during the summer drought in 2020. During the 2022 summer drought the first two lines of admixed species around each wild service tree group were irrigated at Fontmell and Spernal.

The admixed species at Fontmell performed significantly better, both in terms of survival and height growth *(Fig. 10)*. The lower mean heights at Sotterley and Spernal are affected by the high number of replacement seedlings after the first two growing seasons. However, the height increment was most likely stalled for the unreplaced seedlings as well due to the severe drought.

Table 13. Mean height and survival rate for the admixed species at all sites. H_3 = height at the end of the third growing season (2022). Sur_{1-3} = Survival rate (%) after growing seasons 1-3. n= Total number of seedlings in plot design

	Fontmell			Sotterley					Spernal				
Species	H_3 (cm)	n	Sur_{1-3} %	H_3 (cm)	n	Sur_1 %	Sur_2 %	Sur_3 %	H_3 (cm)	n	Sur_1 %	Sur_2 %	Sur_3 %
Field maple	110.8	672	97 >	41.3	672	90	97	99.1	42.7	672	63.5	93.2	97.9
Hornbeam	67.9	1344	97 >	43.9	1344	65.3	67.4	91.7	38.9	1344	45.9	83.8	92.5
Pedunculate oak	56.3	1152	97 >	46.3	1152	69.2	48.5	91.8	40.8	1152	59.5	85.6	91.1
European hazel	-	945	97 >	-	945	78.8	97.9	100	-	945	62.3	99.5	98.5
Mean	78.3		97 >	43.8		75.8	77.7	95.7	40.8		57.8	90.5	95

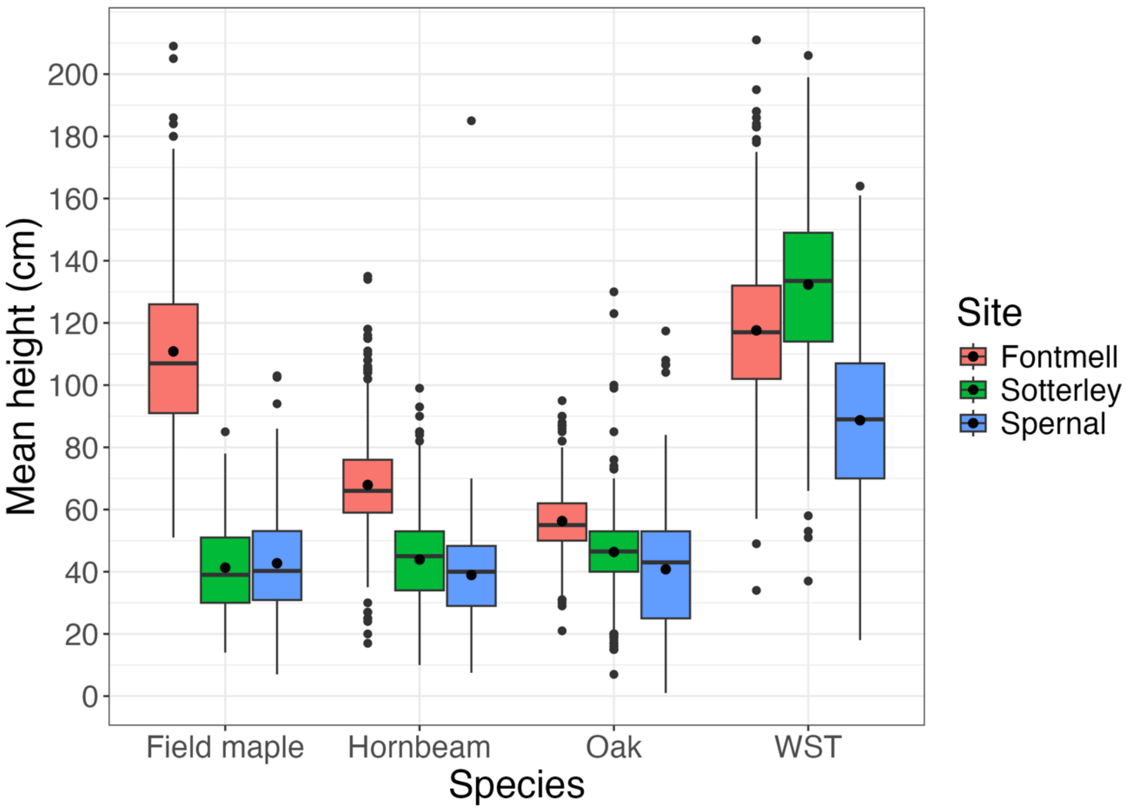

Figure 10. Mean height per species and site after the third growing season, recorded in February 2023. Field maple at Fontmell was irrigated during the summer of 2020. During the summer of 2022 the first two lines of admixed species around each wild service tree group were irrigated at Fontmell and Spernal.

3.1.2 Damage, pests, and general comment per site

Fontmell

Overall, a low occurrence of damage was recorded for the wild service trees. Bark beetle/insect damage was noted on 125 trees after the third growing season, with 100 of them being minor damages with no, or minor effects on tree growth, ten with possible effect on tree growth, and five classed as major damage that had a negative effect on tree growth or stem quality. Minor cankers and/or desiccation were noted on 19 trees in total, these could be caused by the protective tubes creating a "chimney draught" effect leading to a warm and dry microclimate in the tubes, as described by Skovsgaard and Graversgaard (2013c). The competing ground vegetation was quite strong with meadow brome *(Bromus commatus)*, broad-leaved dock *(Rumex obtusifolius)*, and field bindweed *(Convolvulus arvensis)* of most concern. However, the majority of the wild service trees were well established and resilient towards ground vegetation after the fourth growing season.

Blocks 1 and 2, located at the top of the hill, exhibited a higher growth rate compared to other blocks *(Table 25)*. However, during data collection in April 2024, numerous instances of shoot and branch snap-offs were observed in Block 2. A field-based hypothesis suggested that these breakages were caused by wind damage, as there is a gap in the surrounding vegetation on the western side of the site *(Fig. 11)*. This gap may create a wind corridor, directing strong winds toward Blocks 1 and 2, which are more exposed due to their elevated position.

The newly flushed shoots are particularly delicate and susceptible to mechanical damage from strong wind gusts. This wind exposure may also explain the higher incidence of dieback observed in these blocks, as repeated wind stress could contribute to shoot mortality and structural damage in young trees.

Table 14. Summary of fourth-year measurements at Fontmell (mean values per block; original population. Legend: n = Total number of seedlings from original population (144 per block) H_4 = mean height at the end of the fourth growing season (2023). I_{H4} = Fourth-year growth. DBH = Diameter at breast height at the end of the fourth growing season (2023). Dieback/snap = Noted dieback or snapped/broken apical shoots in April 2024 (original population disregarding beat-ups)

Block	n	H_4 cm	I_{H4} cm/y	DBH mm	Apical shoot dieback/snap-off
1	144	162.5	39.8	10	7/7
2	143	170.2	44.9	10.5	14/14
3	139	143.2	34.9	5.2	6/2
4	143	155.2	39.8	8.9	8/2
Total	569	157.8	39.9	8.7	35/25

Figure 11. Satellite imagery of the Fontmell site displaying a gap in the vegetation at the western side of the site (red arrow) creating a wind corridor, possibly causing wind damage to newly flushed shoots in block 1 and 2. (Google Earth, 2022.)

Block 3 seems to have a stunted growth compared to the other blocks; a hypothesis was that the soil could be more compacted by machinery in that end of the site. Block 3 also has the lowest soil assessment score with lower nutrient rates than the other blocks (Appendix 1). Tortoiseshell Wood, Rahay, and Sailershausen at the bottom of the hill seems to be most negatively affected. Sylleptic branching in the top of the apical shoot seemed to be more prominent at this site, however it was not studied consistently at all sites.

Sotterley

Very few cases of damage were recorded at Sotterley. Only one Tortoiseshell Wood tree exhibited a canker or corking of the stem that significantly hindered growth, and one Harcourt tree displayed severe leaning. Competing ground vegetation was less of a concern at Sotterley compared to the other sites.

Blocks 3 and 1 showed the highest growth and survival rates. However, an increased occurrence of dieback was observed in Block 3 after the fourth growing season *(Table 26).* In contrast to the Fontmell site, fewer instances of shoot and branch snap-off were recorded in April 2024. The higher number of snap-offs in Block 1 may be attributed to wind exposure, as this block is more open to prevailing winds *(Fig. 12).* Another hypothesis is that shoot snap-off could be caused by insect activity, possibly the pear-shoot sawfly (*Janus compressus*), as suggested by Coello *et al.* (2013).

Table 15. Summary of fourth-year measurements at Sotterley (mean values per block; original population. Legend: n = Total number of seedlings from original population (144 per block) H_4 = mean height at the end of the fourth growing season (2023). I_{H4} = Fourth-year growth. DBH = Diameter at breast height at the end of the fourth growing season (2023). Dieback/snap = Noted dieback or snapped/broken apical shoots in April 2024 (original population disregarding beat-ups)

Block	n	H_4 cm	I_{H4} cm/y	DBH mm	Apical shoot dieback/snap-off
1	132	180.9	43.9	11.4	4/5
2	128	167.6	38.5	11.4	5/0
3	139	184.1	45	13.1	14/3
4	132	175.7	42.8	11.6	1/3
Total	531	177.1	42.6	11.9	25/11

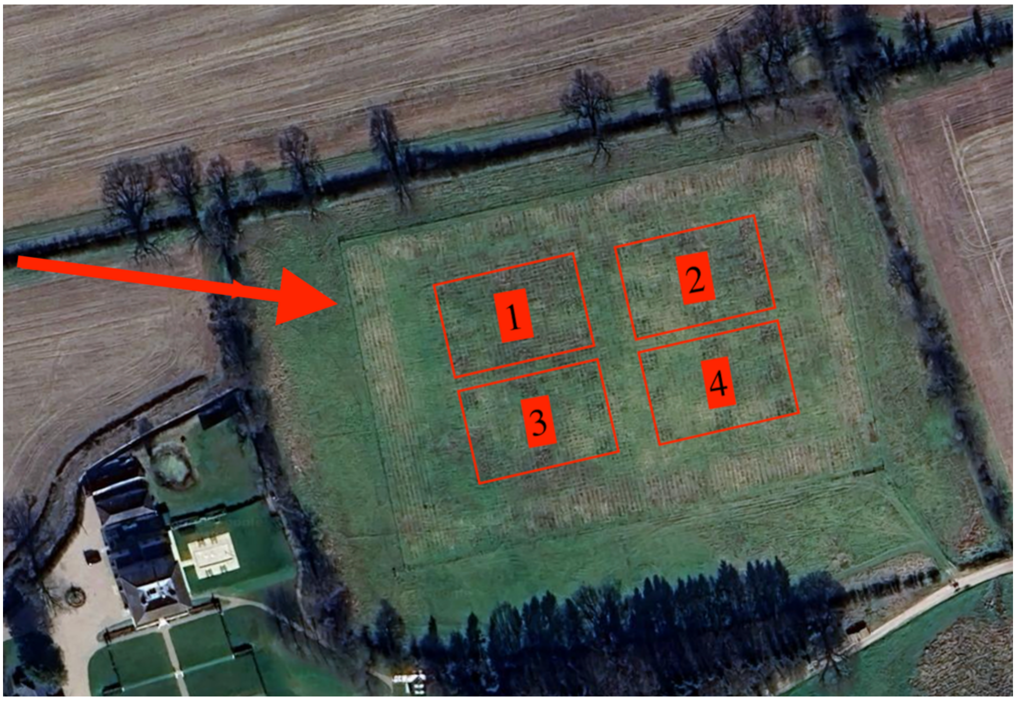

Figure 12. Satellite imagery of the Sotterley site with possible wind damage to newly flushed shoots in blocks 1 and 2 caused by western winds. (Google Earth, 2022).

Spernal

The Spernal site presented less-than-ideal conditions for tree planting. The site is characterized by flat topography with minor depressions, poorly drained gley soils, and marginal groundwater movement, making it prone to both drought and waterlogging. The surrounding land is slightly elevated, which may increase frost risk and contribute to stagnant groundwater.

Competing ground vegetation was most intense at this site, with dense growth of grasses (*Poaceae* spp.), ragwort (*Jacobaea vulgaris*), thistles (*Cirsium* spp.), and broad-leaved dock (*Rumex obtusifolius*), posing significant challenges. Combined with severe drought conditions, these factors hindered seedling establishment during the first growing seasons and may have contributed to the higher proportion of dieback observed at this site.

The occurrence of apical shoot snap-off was very low, with only three trees exhibiting damage in April 2024, possibly due to the site's reduced wind exposure, or due to limited growth resulting in fewer long, and fragile apical shoots. Few cases of severe damage were recorded – eight trees were affected by cankers, half of which appeared to be caused by bark beetles or other insects. However, these instances did not seem to have a significant negative impact on growth or stem quality.

Growth variation between blocks appeared to be lower at Spernal compared to the other sites. Blocks 4 and 2, located in the northern part of the site, exhibited slightly better growth rates and lower mortality *(Table 27)*. Despite the slow start, the wild service trees showed marked improvement by the end of the fourth growing season, which was less dry than previous years.

Table 16. Summary of fourth-year measurements at Spernal (mean values per block; original population. Legend: n = Total number of seedlings from original population (144 per block) H_4 = mean height at the end of the fourth growing season (2023). I_{H4} = Fourth-year growth. DBH = Diameter at breast height at the end of the fourth growing season (2023). Dieback/snap = Noted dieback or snapped/broken apical shoots in April 2024 (original population disregarding beat-ups)

Block	n	H_4	I_{H4}	DBH	Apical shoot dieback/snap-off
		cm	cm/y	mm	
1	126	119.9	29.9	6.7	8/1
2	134	125.7	34.5	7	8/1
3	131	119.8	30.9	7.4	13/1
4	133	131.4	37.9	7.2	9/0
Total	524	124.2	33.3	7.1	38/3

Figure 13. Satellite imagery of the Spernal site. (Google Earth, 2022).

3.2 Height

3.2.1 Mean height and mean height increment

Site effect

Clear differences in mean height between sites were evident across all four growing seasons. After the fourth growing season, Sotterley had a mean height among all seed sources of 177.1 cm, 10.9 % higher than the average at Fontmell (157.8 cm), and 29.9 % higher than the average at Spernal (124.2 cm). A one-way ANOVA confirmed that these differences were statistically significant ($F = 334.7$, $p < 0.001$), indicating that site conditions had a strong effect on mean height. Tukey's post-hoc test further revealed that all three sites were significantly different from each other ($p < 0.001$). Additionally, when analysing mean height across all growing seasons, a similar trend was seen. A separate ANOVA on height increment showed a significant site effect ($F = 261.5$, $p < 0.001$). Tukey's HSD test indicated that trees at Sotterley experienced a significantly greater height increment than those at Fontmell (19.2 cm, $p < 0.001$), while trees at Spernal had the smallest height increment, with 50.7 cm less growth compared to Sotterley ($p < 0.001$).

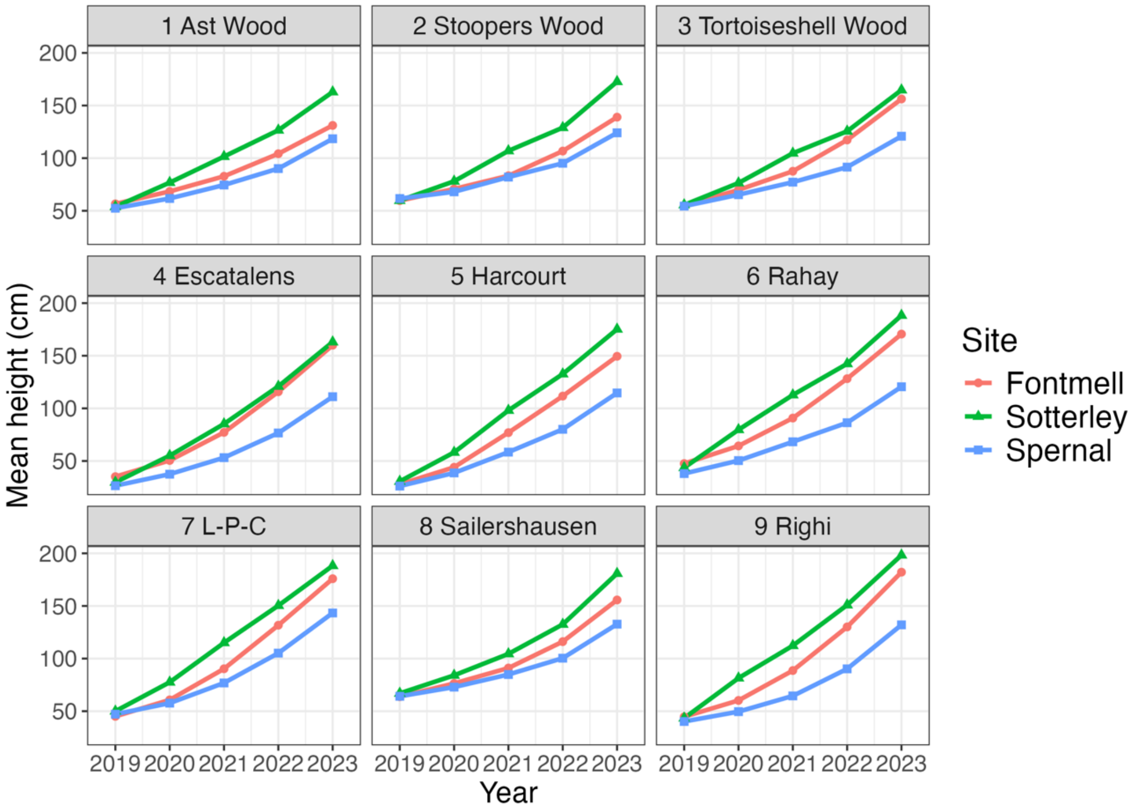

Figure 14. Mean height per seed source and site from establishment in 2019 to winter 2023. Original population disregarding beat-ups (n=1624).

Seed source effect

A clear difference in mean height between seed sources was evident as well. Righi (172.5 cm) had the highest total mean height across all sites after the fourth growing season, followed by L-P-C (169.2 cm) and Rahay (161.9 cm). Sailershausen (156.1 cm) was close to the overall mean height of all seed sources (153.4 cm). Ast Wood had the lowest mean height (137.3 cm), while Stoopers Wood (144.6 cm) and Escatalens (145.5 cm) were the second and third shortest, respectively. This represents a 19.5 % difference in total mean height between the best- and worst performing seed sources. A one-way ANOVA confirmed that seed source significantly influenced mean height after the fourth growing season ($F = 18.02$, $p < 0.001$). Tukey's post-hoc test revealed that Righi, L-P-C, and Rahay exhibited a significantly greater mean height, outperforming Ast Wood, Stoopers Wood, Escatalens, and Harcourt ($p < 0.001$). Meanwhile, Sailershausen, while taller than these seed sources, was significantly shorter than Righi and L-P-C, and only significantly taller than Ast Wood.

Total mean height increment across all sites was also significantly influenced by seed source, confirmed by a one-way ANOVA ($F = 39.88$, $p < 0.001$). Tukey's post-hoc test revealed that Righi (129.6 cm) and L-P-C (121.8 cm) exhibited a significantly greater total mean height increment than Ast Wood (83 cm), Stoopers Wood (84.3 cm), Tortoiseshell Wood (92.4 cm), and Sailershausen (91.2 cm) ($p < 0.001$). The best performing seed source Righi, showcased a 56 % (46.6 cm) higher total mean height increment than the worst performing Ast Wood. Additionally, Righi grew significantly better than Escatalens (114.8 cm) ($p = 0.0098$). However, Righi and L-P-C did not differ significantly from each other ($p = 0.609$), indicating similar growth performance. Neither Righi nor L-P-C differed significantly from Rahay, Harcourt, or Escatalens, suggesting that these seed sources achieved comparable height increments over the four growing seasons.

Most seed sources at Fontmell and Spernal exhibited a steady annual increase in height increment, except for Stoopers Wood at Spernal which had a minimal decrease in 2022 *(Fig. 15).* A larger variation between, and within seed sources was observed at Sotterley. Only Escatalens, Sailershausen, and to some extent Ast Wood had a similar growth pattern at Sotterley with an increasing annual increment. This was thought to be an effect of apical shoot dieback. However, a similar pattern could be seen when the top five trees per plot (tallest total height in 2023, without apical dieback, shoot-snap off, or a negative annual height increment) was plotted *(Fig. 16).* Stoopers Wood, Tortoiseshell Wood, Harcourt, Rahay, and L-P-C saw a decrease in height increment during the 2022 growing season, which was very hot and dry at Sotterley.

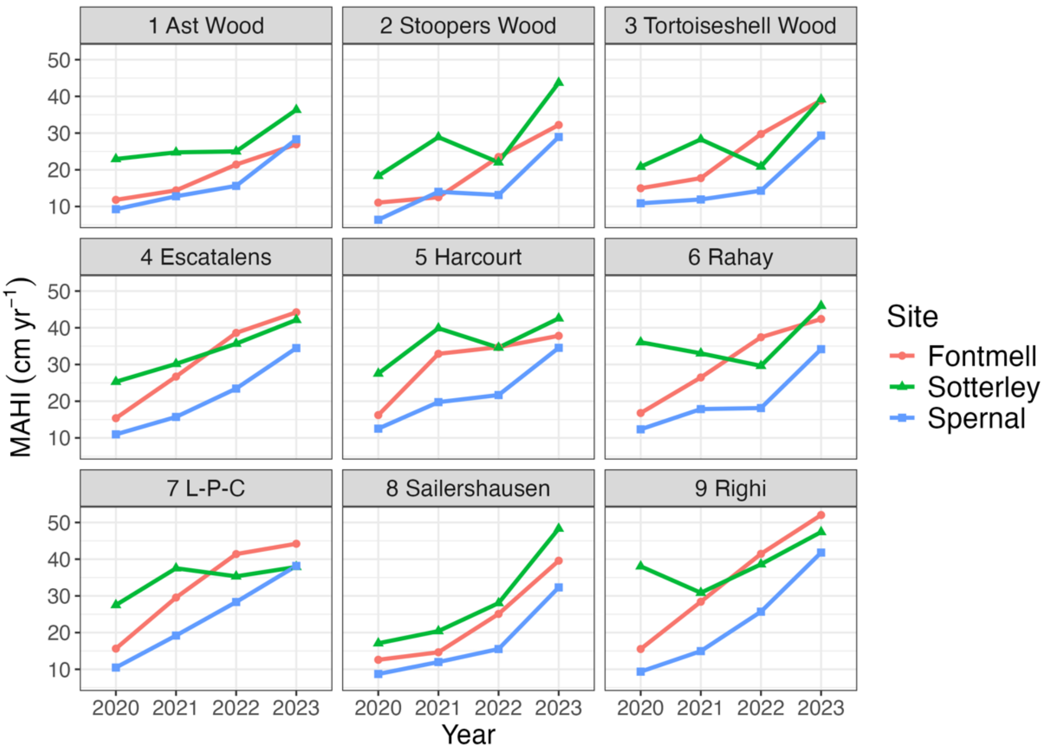

Figure 15. Mean annual height increment per seed source and site from establishment in 2019 to winter 2023. Original population disregarding beat-ups (n=1624).

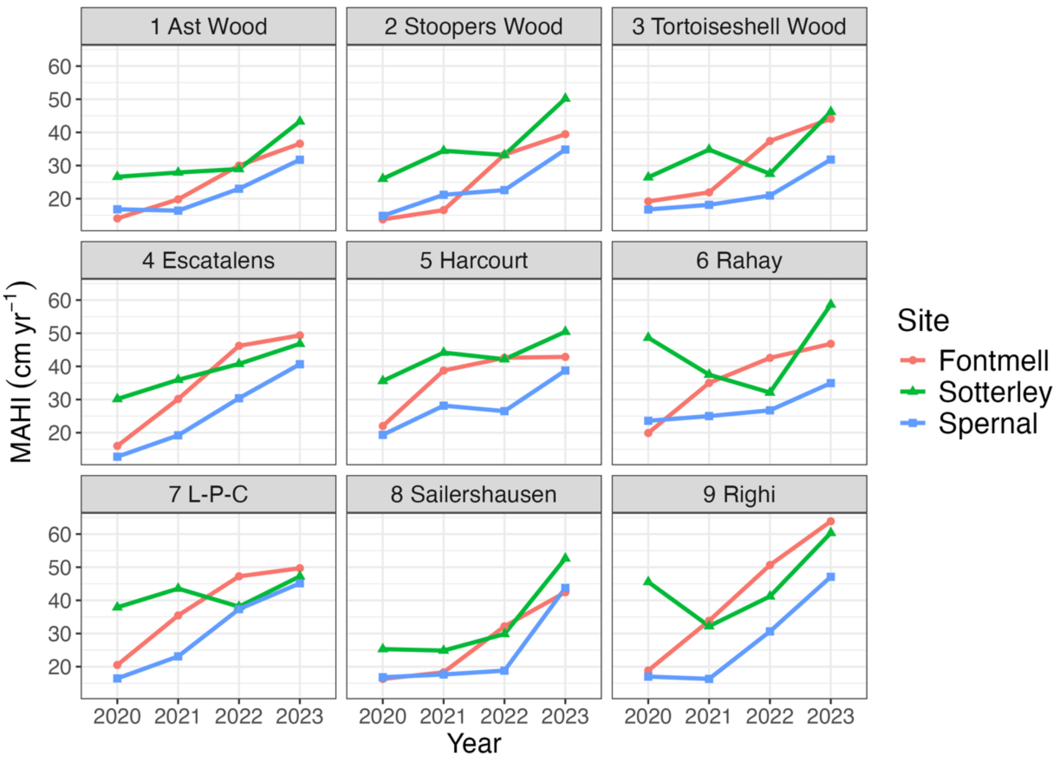

Figure 16. Mean annual height increment per seed source and site from establishment in 2019 to winter 2023. Top 5 trees per plot, original population disregarding beat-ups (n=540).

Correlation between initial height and height increment

Seedlings with a smaller initial mean height appeared to exhibit compensatory growth, particularly Righi, L-P-C, and Rahay, which started with lower initial heights but became the three tallest seed sources on average by the third and fourth growing seasons. In contrast, Escatalens and Harcourt, which had the smallest initial seedling heights, remained among the shortest seed sources after the fourth growing season, but still achieved greater height increments than the English seed sources, ultimately reaching a similar total mean height.

To assess the relationship between initial seedling height and total mean height increment, a correlation analysis was performed, comparing initial seedling height at establishment with total mean height increment after the third growing season across all sites. A negative correlation (R-value) indicates that seedlings with smaller initial heights exhibited greater height increments. This trend was observed in almost all seed sources, except for Escatalens and Harcourt. The strongest negative correlations were found in the three English seed sources and L-P-C, all of which had an R-value below -0.30, suggesting a moderate compensatory growth effect. In contrast, Righi, Rahay, and Sailershausen had R-values closer to zero, indicating little to no correlation between initial height and growth increment.

Table 17. Analysis of correlation between initial seedling height and total mean height increment after three growing seasons (2019-2022). Mean value per seed source at all three sites. Original population, disregarding beat-ups. p-value adjustment method: Holm (1979)

Seed source	Initial seedling height (cm)	Total mean height increment 2019-2022 (cm)	n	R-value	95 % CI	p-value
1 Ast Wood	54.3	52.6	184	-0.31	[-0.44. -0.18]	< .001***
2 Stoopers Wood	60.3	49.5	179	-0.40	[-0.52. -0.27]	< .001***
3 Tortoiseshell Wood	54.9	56.6	187	-0.36	[-0.48. -0.23]	< .001***
4 Escatalens	30.7	74.3	174	-0.003	[-0.15. 0.15]	> 0.999
5 Harcourt	28.2	79.8	180	0.03	[-0.12. 0.18]	0.801
6 Rahay	43.4	77.4	179	-0.21	[-0.34. -0.06]	0.020*
7 L-P-C	47.4	81.7	183	-0.33	[-0.45. -0.19]	< .001***
8 Sailershausen	65	61.2	182	-0.23	[-0.36. -0.09]	0.009**
9 Righi	42.9	82.2	176	-0.14	[-0.28. 0.01]	0.207
Total	47.5	68.4	1624	-0.38	[-0.42. -0.34]	< .001***

After the fourth growing season, the overall correlation weakened, with an R-value of -0.22, compared to -0.38 after the third growing season. At this stage, no individual seed source showed a statistically significant correlation between a smaller initial seedling height and greater height increment. Only Escatalens showed significance but with a positive R-value of 0.29 ($p < 0.001$), indicating that taller seedlings grew more than smaller ones.

Table 18. Min, mean, and max values of initial seedling height per seed source at all sites

Seed source	Min initial height (cm)	Mean initial height (cm)	Max initial height (cm)	Total height increment 2019-2023 (cm)
1 Ast Wood	38	54.3	92	83
2 Stoopers Wood	43	60.3	96	84.3
3 Tortoiseshell Wood	37	54.9	79	92.4
4 Escatalens	13	30.7	64	114.8
5 Harcourt	16	28.2	56	118
6 Rahay	22	43.4	84	118.6
7 L-P-C	25	47.4	83	121.8
8 Sailershausen	33	65	97	91.2
9 Righi	22	42.9	67	129.6
Mean	27.7	47.5	79.8	105.8

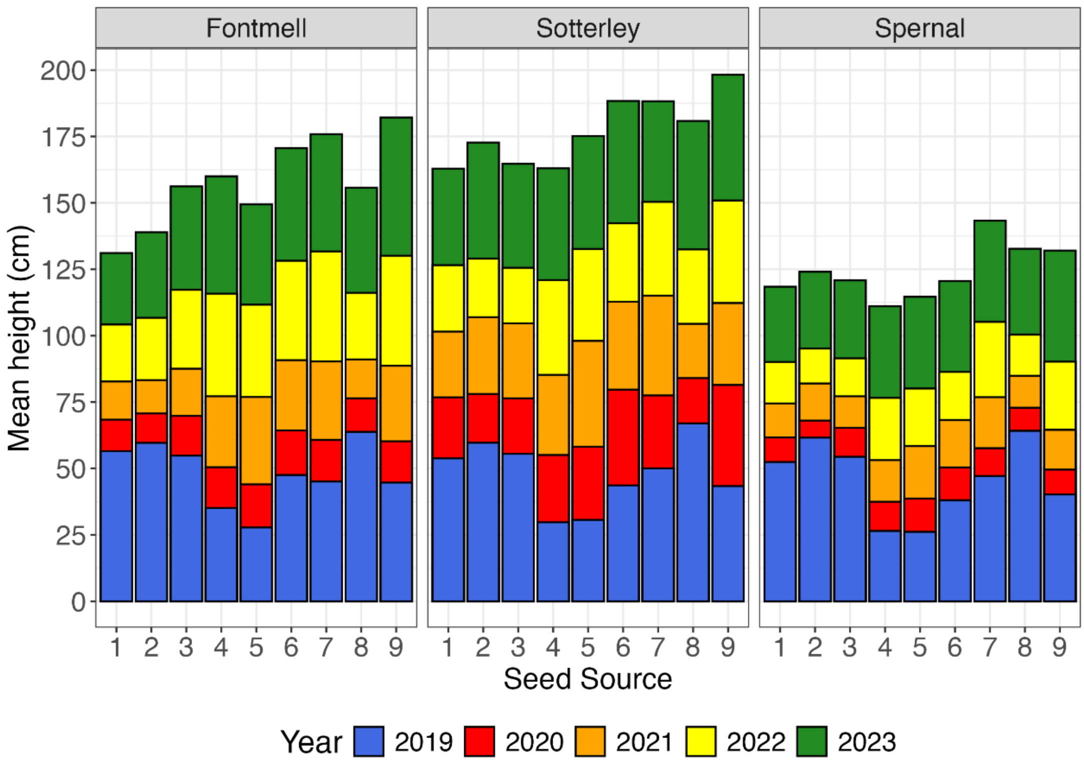

Figure 17. Mean height per seed source and site from establishment in 2019 to winter 2023, blue representing the mean seedling height at establishment. Original population disregarding beat-ups (n=1624).

Site effect model

To further analyse the effects of site conditions on height increment, a linear mixed-effects model (LMM) using restricted maximum likelihood (REML) estimation was fitted. The model structure included both genetic and environmental factors influencing annual height increment, incorporating interactions between initial height, precipitation, and soil fertility. Analysis was performed on the original population *(n=1624)* and the top 5 trees in each plot *(n=540).*

Model structure

$$
\begin{aligned}
IH_ijt = \beta_0 + \beta_1(SS_i) + \beta_2(Hstart_j) + \beta_3(SS_i \times Hstart_j) + \beta_4(W5_t) \\
+ \beta_5(CEC_j) + \beta_6(W5_t \times CEC_j) + \beta_7(CNratio_j) \\
+ \beta_8(W5_t \times CNratio_j) + u_j + \epsilon_ijt
\end{aligned}
$$

The analysis revealed that seed source had a significant effect on height increment in both the subset ($p = 0.0032$) and the full dataset ($p < 0.0001$), confirming that genetic differences influence growth. Initial seedling height at planting was also a key predictor, with taller trees maintaining a significant advantage in both datasets ($p < 0.0001$). Environmental factors, particularly precipitation and irrigation *(W5)*, and soil fertility *(CEC),* were also strong drivers of growth, both showing highly significant effects ($p < 0.0001$). The interaction between water availability and soil fertility *(W5 × CEC)* further indicated that trees growing in more fertile soils utilized water more efficiently, suggesting an important synergy between these two site characteristics.

While the Carbon-to-Nitrogen ratio *(CNratio)* showed no significant effect in the subset analysis ($p = 0.2557$), it was significant in the full dataset ($p = 0.0239$). This suggests that soil organic matter balance may play a role in growth, but the effect was not strong enough to be detected in the smaller subset. Meanwhile, the interaction between *CNratio* and precipitation *(W5 × CNratio)* remained non-significant in both datasets, indicating that the influence of organic matter on tree growth does not appear to be mediated by water availability.

A notable finding was the interaction between seed source and initial height *(SS × Hstart),* which was significant in both datasets ($p = 0.0148$ in the subset and $p = 0.0025$ in the full dataset). This suggests that the effect of initial height on growth varies between seed sources, with some seed sources benefiting more from a taller start height.

Table 19. Significance and interpretation of fixed effects. Top 5 subset (n=540) and full dataset (n=1624). W5=Annual precipitation and irrigation (April-August)

Predictor	Subset (p-value)	Full Dataset (p-value)	Interpretation
Seed source (*SS*)	0.0032	<0.0001	Significant effect on annual height increment
Initial height *(Hstart)*	<0.0001	<0.0001	Indicating an advantage in growth for taller seedlings at establishment
Precipitation & irrigation *(W5)*	<0.0001	<0.0001	Water availability is a key driver of growth
Soil Cation Exchange Capacity *(CEC)*	<0.0001	<0.0001	Higher soil fertility enhances growth
W5 × *CEC* Interaction	<0.0001	<0.0001	Water availability interacts with soil fertility, suggesting that soil properties influence utilization of water
SS × *Hstart* Interaction	0.0148	0.0025	Effect of initial height on growth varies depending on seed source
Soil Carbon:Nitrogen Ratio *(CNratio)*	0.2557 (NS)	0.0239	Significant in the full dataset – suggesting an effect not detected in the subset
W5 × *CNratio* Interaction	0.2951 (NS)	0.1101 (NS)	No significant interaction between soil C:N ratio and precipitation.

The comparison of height increments among seed sources highlights substantial genetic differences in growth potential. Across both datasets, Righi, L-P-C, and Rahay consistently ranked as the top performers, with Righi achieving the highest estimated height increment (35 cm in the subset and 28.8 cm in the full dataset). These seed sources demonstrated superior growth, suggesting that their genetic makeup is particularly well-suited to the environmental conditions of the trial sites.

In contrast, Ast Wood consistently had the lowest growth rate, with an estimated increment of 27 cm in the subset and only 21.4 cm in the full dataset. This indicates that Ast Wood trees generally struggled to compete in the given conditions, either due to genetic limitations, poor adaptation to site conditions, or inherently slower growth rates. The lack of significant improvement in the top 5 dataset suggests that even the best individuals from this seed source did not perform at the level of other seed sources.

Table 20. Height increment estimate, standard deviation (SD) and coefficient of variation (CV). Top 5 subset (n=540) and full dataset (n=1624)

Seed Source	Subset Estimate (cm)	Full Dataset Estimate (cm)	Subset SD (cm)	Full Dataset (cm)	Subset CV (%)	Full Dataset CV (%)
9 Righi	35	28.8	21	19.5	60	67.7
7 L-P-C	34.8	28.5	17.3	18	49.7	63.1
6 Rahay	33.8	26.5	17.9	19.1	53	72.1
5 Harcourt	33.6	27.2	16.4	16.6	48.8	61
8 Sailershausen	32.3	25.4	18.2	19.3	56.4	75
4 Escatalens	30.8	26.1	16.8	16.3	54.6	62.5
3 Tortoiseshell Wood	28.4	23.4	13.8	15.1	48.6	64.5
2 Stoopers Wood	29.3	22.9	15.5	17	52.9	74.2
1 Ast Wood	27	21.4	12.2	13.4	45.2	62.6

While Righi exhibited the highest growth rate, it also showed among the highest variation. This suggests that while some trees within this seed source performed exceptionally well, others were falling behind. L-P-C demonstrated strong growth but with lower variation, indicating a more stable performance. Rahay also performed well but exhibited higher variation, especially in the full dataset, meaning that while most trees from this seed source are strong growers, there is still some degree of variability in performance.

Among the moderate performers, Harcourt and Escatalens showed slightly below-average growth but relatively stable performance. At the lower end of the spectrum, Tortoiseshell Wood, Stoopers Wood, and Ast Wood showed below-average growth, but with different levels of stability. Ast Wood had among the lowest variation meaning it produced more uniform trees, while Stoopers Wood had a more uneven growth.

The differences in standard deviation (SD) and coefficient of variation (CV %) across seed sources may partly reflect the genetic variation within each seed source, but also site-specific factors that were not explicitly modelled, such as slope inclination, competing ground vegetation, microclimate, and temperature variations. These uncontrolled environmental variables may have increased the variability in tree growth within certain seed sources by disproportionately affecting individual trees at different locations within the sites. For example, seed sources with high variation (such as Righi and Sailershausen) might be more sensitive to these factors, leading to a wider range of individual performances.

3.3 Apical shoot dieback

Apical shoot dieback per site

The apical shoot dieback was noticeably higher at the Spernal site throughout the first three growing seasons *(Fig. 18)*. After the first growing season, 23 % of the seedlings at Spernal were recorded with apical shoot dieback. At Fontmell (9 %) and Sotterley (7 %) less than 10 % of the seedlings were recorded with dieback after the first growing season.

After the second growing season, all three sites saw a lower proportion of apical shoot dieback with Spernal just below 20 %. At Fontmell and Sotterley it was close to 5 %. The trend of diminishing dieback seemed to persist during the third growing season with Spernal below 15 % and Sotterley at around 5 %. Only Fontmell had a rise in dieback with 9 % recorded after the third growing season. After the fourth growing season, around 5 % of dieback was recorded at all sites.

Over the full trial period, 80.4 % of the trees at Sotterley and 76.6 % at Fontmell showed no dieback at any time, while this was true for only 58.6 % at Spernal, further underlining the adverse site conditions affecting long-term vitality at this location.

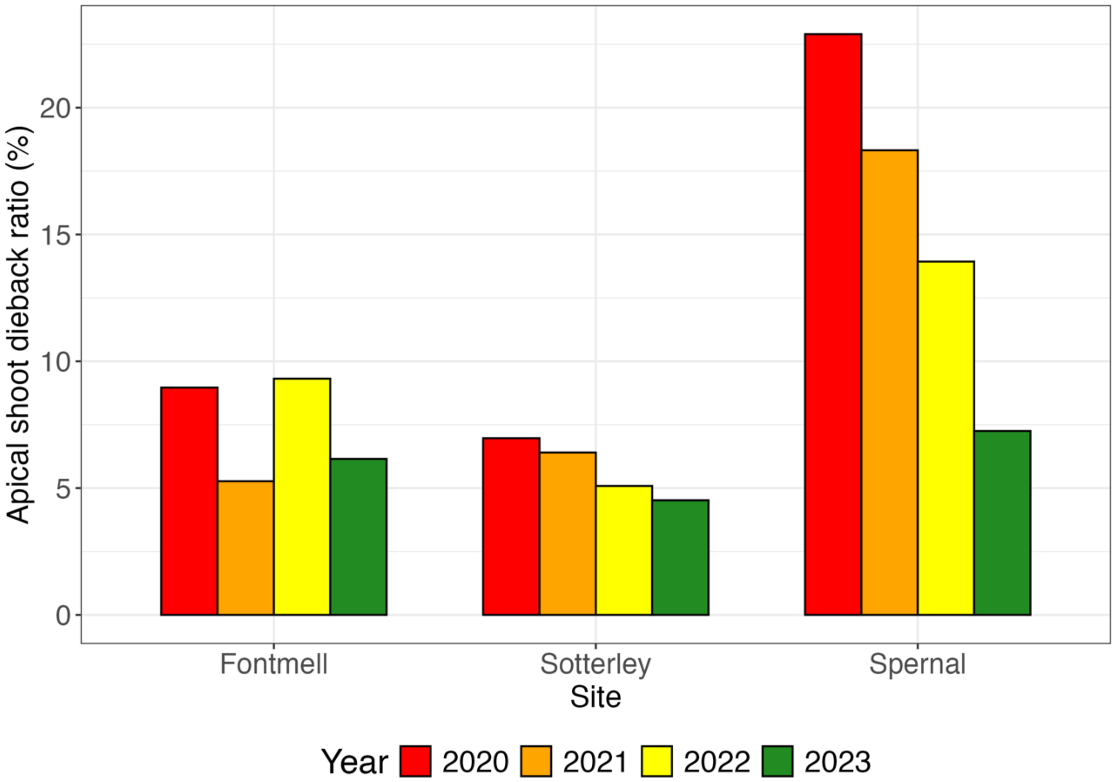

Figure 18. Proportion of apical shoot dieback at all sites, recorded in winter after each growing season. Original population disregarding beat-ups (n=1624).

Apical shoot dieback per seed source

The English seed source Stoopers Wood clearly had the highest amount of dieback during the first growing season with almost 25 % *(n=51)* of the total recorded dieback, with 51 % occurring at Spernal. At Fontmell and Sotterley 24.5 % *(n=12)* of dieback was recorded for Stoopers Wood respectively. L-P-C had a significantly lower proportion of dieback in the second and third growing season with less than 5 % recorded on average at all three sites.

The Italian and French seed sources had the lowest amount of dieback with nearly all seed sources below 10 % (except Righi in 2020 and Rahay in 2021), while the English seed sources, accompanied by Sailershausen, had a significantly higher proportion of dieback throughout the first three growing seasons with over 10 % recorded each year (except for Ast Wood in 2022). The fourth growing season showcased the lowest occurrence of dieback for all seed sources, except for L-P-C and Harcourt which had a minor increase of dieback. In general, the apical shoot dieback was low and mainly a problem at the Spernal site.

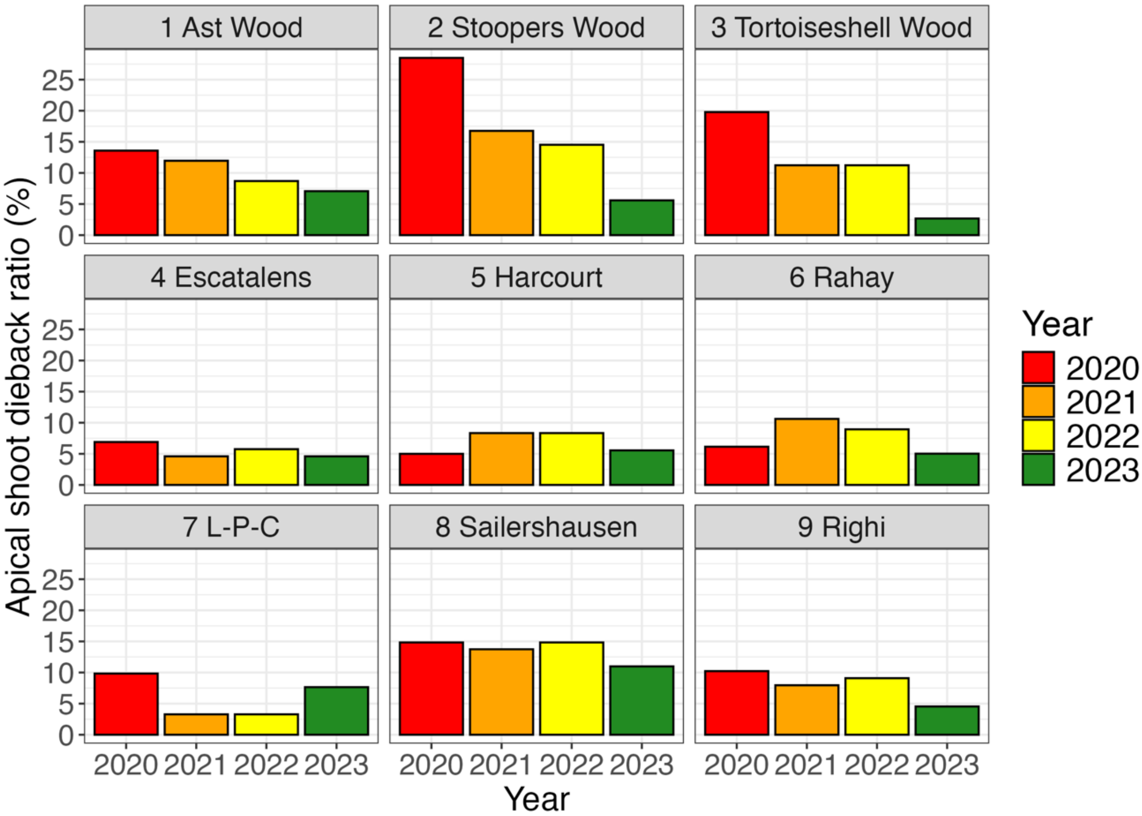

Figure 19. Proportion of apical shoot dieback per seed source at all sites, recorded in winter after each growing season. Original population disregarding beat-ups (n=1624).

Correlation between apical shoot dieback and height growth

A Spearman correlation analysis revealed a significant negative relationship between apical shoot dieback and height increment for all four growing seasons. The correlation was strongest in 2020 ($\rho = -0.458$, $p < 0.001$) and decreased in strength in subsequent years: 2021 ($\rho = -0.315$), 2022 ($\rho = -0.250$), and 2023 ($\rho = -0.145$), all with $p < 0.001$. This pattern suggests that apical damage had a stronger impact on height growth during the first growing season, but that the trees could partially recover or compensate in later growing seasons.

3.4 Forking frequency

Forking frequency per site

The occurrence of forks was considerably higher at the Spernal site where 26 % of the wild service trees were recorded with at least one fork. At Fontmell and Sotterley 14.6 % and 15.2 % were recorded respectively.

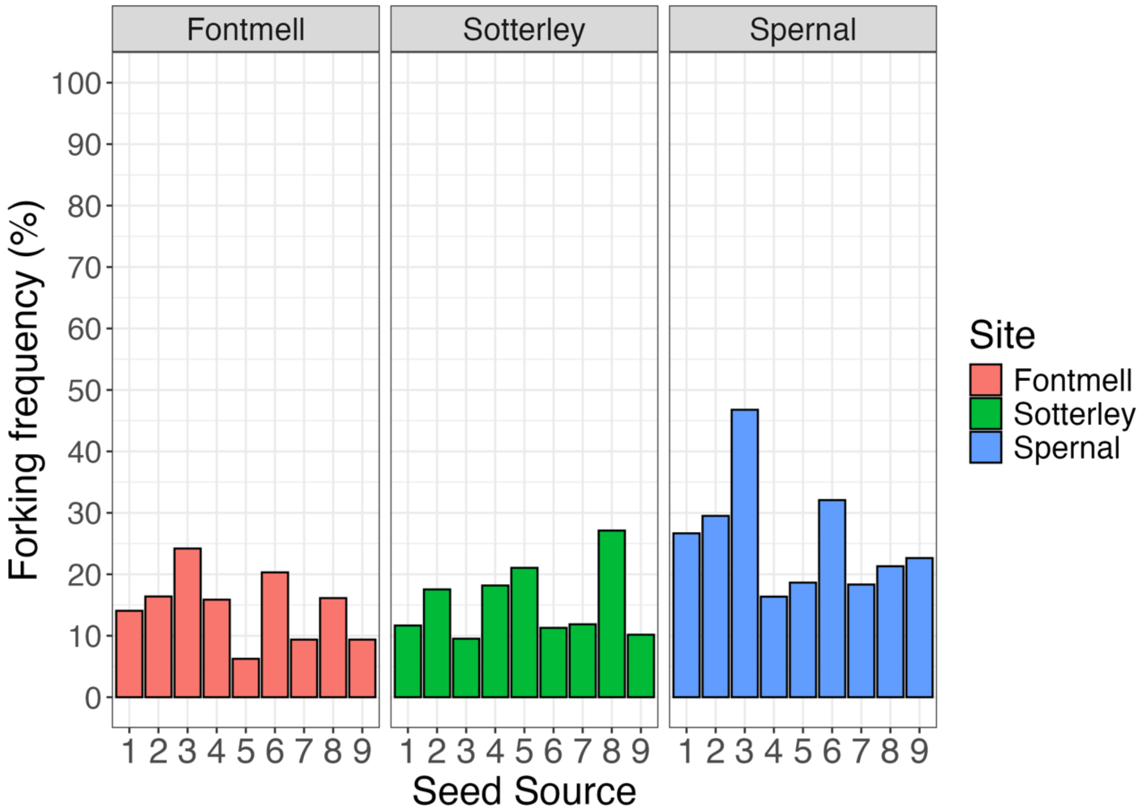

Figure 20. Forking frequency (%) per seed source and site, recorded in February 2023. Original population disregarding beat-ups (n=300).

Forking frequency per seed source

L-P-C and Righi had the lowest occurrence of forks at all sites with 13.1 % and 13.6 % respectively. Among the English seed sources, Ast Wood had the lowest number of forks with 17.7 % recorded. Tortoiseshell Wood had a significantly higher proportion of forks with 26.7 % (50 trees in total), Sailershausen had the second highest amount of forks with 21.4 % recorded at all sites, as well as the highest amount at Sotterley with 27.1 %. In general, the occurrence of forks was quite low with most seed sources below or around 20 %, with a high proportion at the Spernal site.

Correlation between apical shoot dieback and forking

To test if there was a correlation between apical shoot dieback and forking, a chi-squared test was performed. The analysis revealed a strong and highly significant association between apical shoot dieback and forking frequency ($\chi^2 = 83.066$, df = 1, $p < 2.2e-16$). Trees with recorded apical shoot dieback during the first three growing seasons were more than twice as likely to develop a fork compared to those without dieback. Among the 384 trees that suffered apical dieback, 132 (34.4 %) developed a fork, whereas only 168 out of 1240 trees (12.7 %) without dieback exhibited forking.

Table 21. Contingency table of apical shoot dieback during first three growing seasons, and forks recorded in February 2023. Original population disregarding beat-ups (n=1624)

	Fork	No fork	Total
Apical shoot dieback	132	252	384
No apical shoot dieback	168	1072	1240
Total	300	1324	1624

3.5 Diameter at breast height and diameter of thickest branch

Diameter at breast height 2022

Sotterley had a slightly larger mean DBH (6.2 mm) than Fontmell (5.4 mm). A large variation was found within seed sources, with the largest diameters and variation within seed sources at Sotterley. Righi, Sailershausen, L-P-C, and Rahay had the largest diameters on average, as well as large variations. Ast Wood and Stoopers Wood had the smallest diameters on average with a larger variance towards other seed sources at Fontmell where Tortoiseshell Wood clearly had the largest diameter of the English seed sources *(Fig. 21)*.

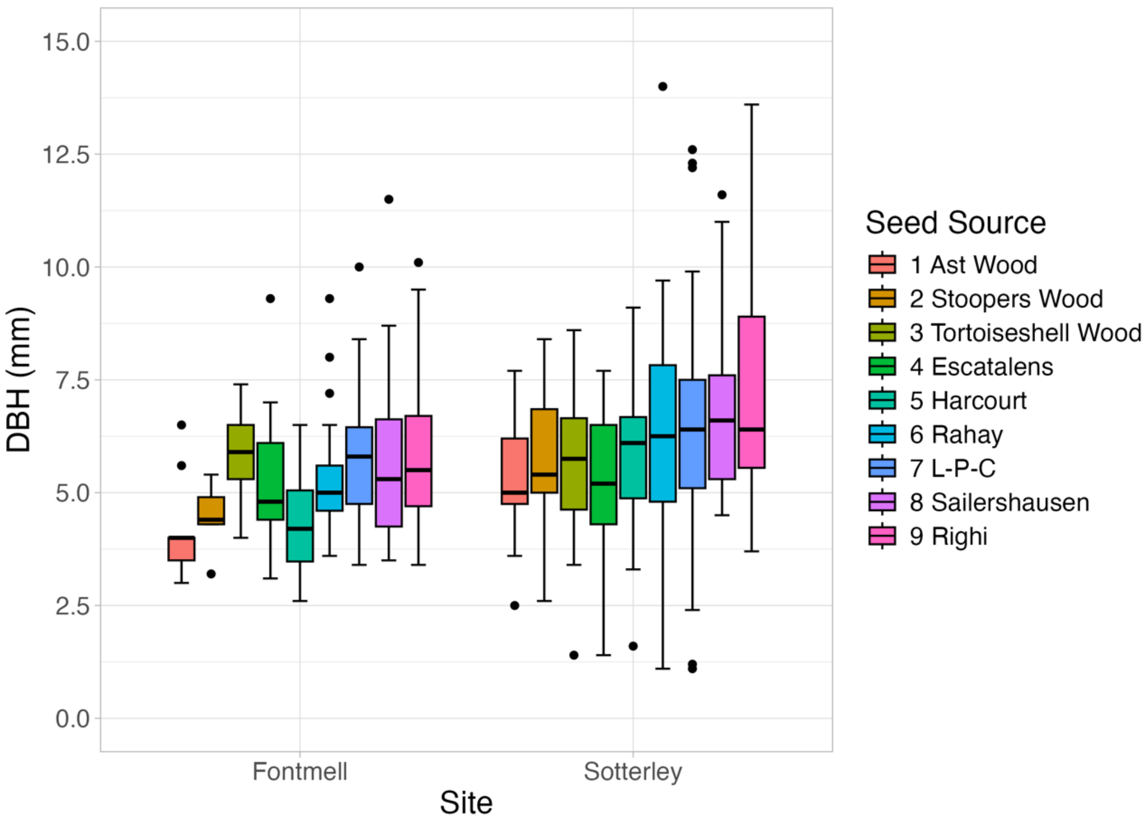

Figure 21. Mean diameter at breast height (mm), per seed source at Fontmell and Sotterley, recorded in February 2023. Original population disregarding beat-ups (n=469).

Diameter at breast height 2023

The total mean DBH for all seed sources at all sites increased from 5.9 mm to 9.4 mm. Excluding Spernal in the 2023 data, the mean DBH was 10.2 mm meaning the DBH roughly doubled in the 2023 growing season. The largest diameter and variation were again recorded at Sotterley. Righi, Sailershausen, L-P-C, and Rahay had the largest diameters measuring over 10 mm on average, as well as large variations, with the largest recorded diameter at 30 mm for a Righi tree. At Fontmell only Righi had a mean DBH above 10 mm.

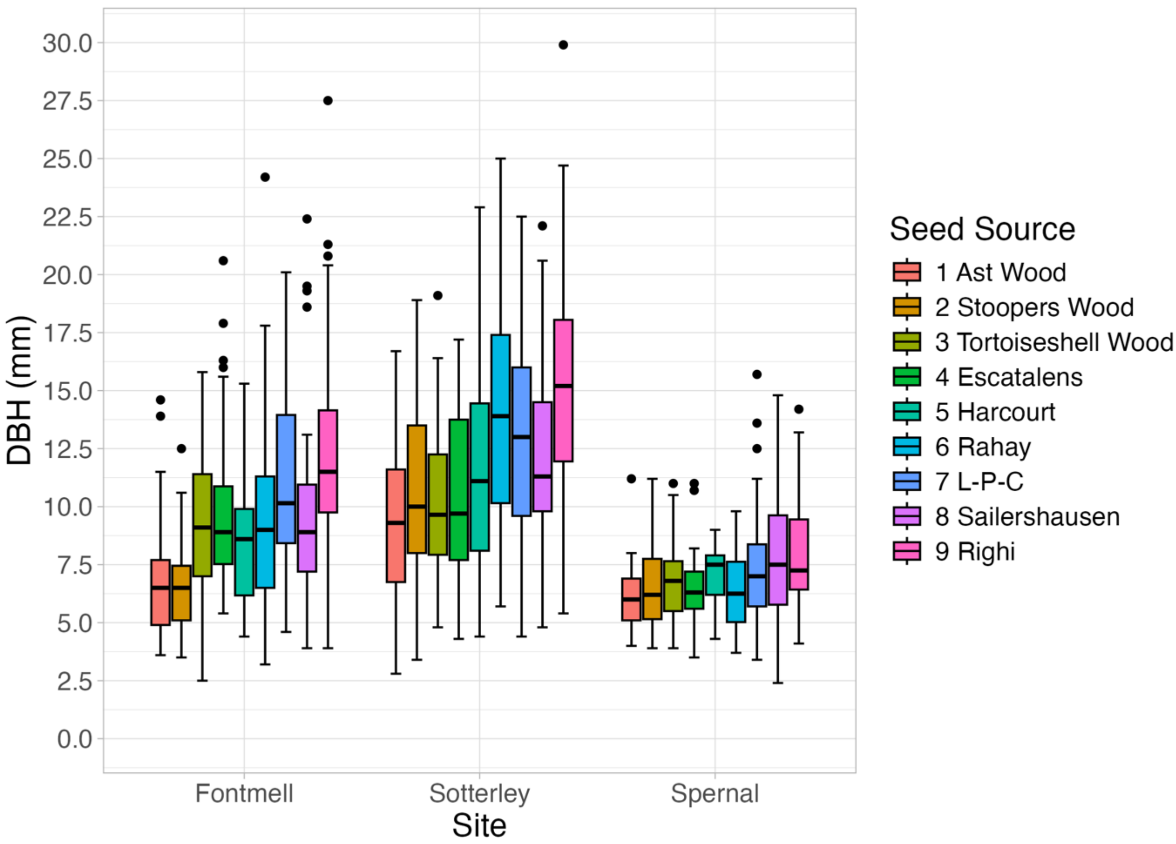

Figure 22. Mean diameter at breast height (mm), per seed source and site, recorded in April 2024. Original population disregarding beat-ups (n=1177).

A one-way ANOVA demonstrated highly significant differences in DBH between seed sources ($p < 0.0001$), confirming genetic variation in growth potential. Additionally, site effects were highly significant ($p < 0.0001$), indicating that environmental factors strongly influence DBH growth. A significant Seed Source × Site interaction ($p = 0.000018$) further suggests that some seed sources perform better at specific sites, rather than exhibiting consistent growth across all locations.

A Tukey's HSD test revealed that Righi had significantly larger DBH values compared to nearly all other seed sources ($p < 0.0001$), reinforcing its superior growth. L-P-C and Rahay also significantly outperformed several lower-ranked seed sources, including Ast Wood and Stoopers Wood. No significant differences were found between Tortoiseshell Wood, Escatalens, and Harcourt, positioning them as moderate performers.

Diameter of thickest branch

The diameter of the thickest branch (DTB) varied considerably between seed sources, with an overall mean DTB of 6 mm across all sites. The largest branch diameters were observed in Rahay, Sailershausen, L-P-C, and Tortoiseshell Wood, with mean DTB values exceeding 6 mm. Ast Wood, Stoopers Wood, and Escatalens had the smallest branches, with mean DTB values below 5.7 mm.

A Levene's test for homogeneity of variance was conducted. The test was non-significant ($p = 0.2531$), indicating that variance in DTB did not differ significantly between seed sources. This suggests that while DTB differences exist between seed sources, the spread of values within each seed source is relatively similar. Variation within seed sources was assessed using the coefficient of variation (CV), which showed the highest variation in Harcourt (CV = 43.2%), followed by Escatalens (38.3%) and Rahay (37.4%). Tortoiseshell Wood (26.1%) had the lowest variation, suggesting a more uniform growth pattern. An ANOVA was performed to assess whether mean DTB differed significantly across seed sources and sites. The results showed a significant effect of both seed source and site ($p < 0.001$), confirming that both genetic and environmental factors influence DTB. Additionally, a significant Seed Source × Site interaction ($p < 0.05$) suggests that the effect of seed source on branch thickness varies depending on the site conditions.

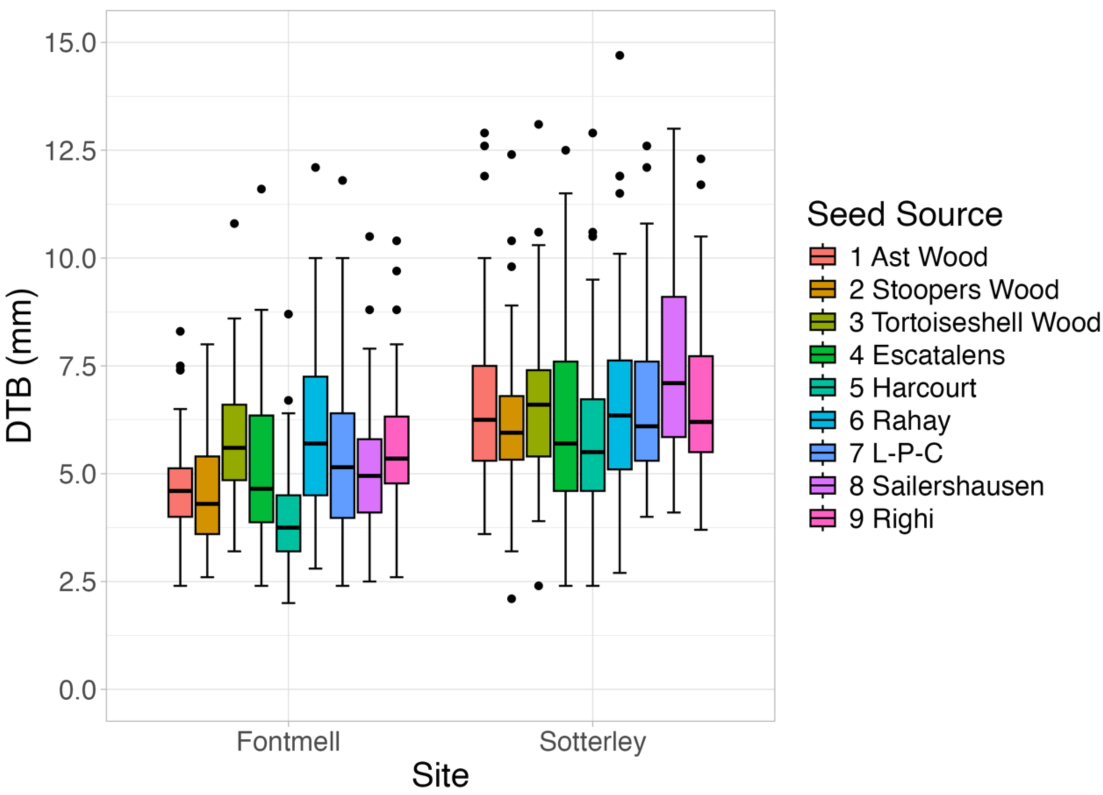

Figure 23. Mean diameter of thickest branch (mm), per seed source and site at Fontmell and Sotterley, recorded in February 2023. Original population disregarding beat-ups (n=1100).

3.6 Stem form and future crop tree

Stem form variation across sites and seed sources

Significant differences in stem form were observed among both sites and seed sources. At Sotterley over 70 % of the stems were ranked in the top three classes (1.5, 2, and 2.5), meaning the stems were straight, or nearly straight in two planes. Sotterley also had the highest proportion (20 %) of stems classified as 2.5, where a spiralling base straightened further up the stem. Fontmell followed with 60 % of trees in the top three classes, of which approximately a third were ranked as 2.5. Spernal had the lowest proportion of straight stems, with about half classified in the top three classes with 10.9 % ranked as 2.5.

Harcourt exhibited the highest proportion of straight stems across all sites (73 %), followed closely by Righi, L-P-C, and Escatalens. Sailershausen had the highest proportion of stems ranked as straight in two planes, while L-P-C and Righi had a significantly larger share of stems graded as 2.5. This was evident for the French seed sources and Righi that were sown late. Righi at Sotterley stands out with 92 % of the trees ranked in the top three classes, of which 44 % were ranked as 2.5 and 30 % as 2. The English seed sources were generally ranked lower, with around half of the trees in the top three classes.

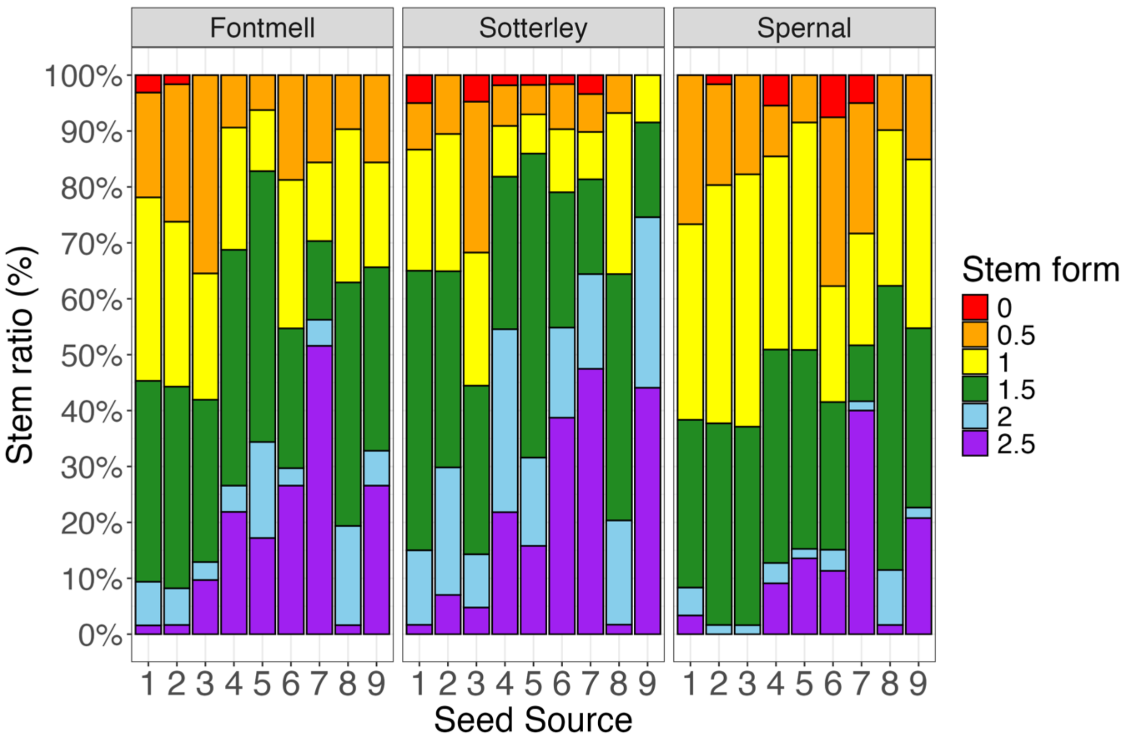

Figure 24. Stem straightness per seed source and site in February 2023. Stem straight in 0, 1 or 2 planes, or intermediate between these (0.5 and 1.5); 2.5 stems with score 0 or 0.5 at the base / in the tube and score 2 above the tube. Original population disregarding beat-ups (n=1624).

Statistical analysis of stem form (SF) was performed on the original population *(n=1624)* and the top 5 dataset used in the height increment analysis *(n=540)*. Significant variation across seed sources and sites was revealed, highlighting the influence of genetic and environmental factors on tree morphology. The stems classified as 2.5 (spiralling base) were reclassified as 2 when calculating the mean stem form, comprising 62.4 % of trees classified as straight in two planes.

A two-way ANOVA confirmed highly significant effects of seed source ($p < 0.001$) and site ($p < 0.001$) on stem form in the original population. Additionally, a small but significant interaction between seed source and site ($p = 0.00014$) was detected, indicating that the performance of different seed sources varied across locations. For the top 5 dataset seed source and site remained highly significant ($p < 0.001$), but the seed source × site interaction was non-significant ($p = 0.172$), indicating greater stability in seed source rankings across sites when considering only the top-performing individuals.

Levene's test indicated that variance in stem form differed significantly among seed sources in the original population ($p < 0.001$), meaning that some seed sources had more variation in stem form than others. Among the seed sources, Tortoiseshell Wood (CV = 45.1 %), Rahay (44.5 %), and L-P-C (41.3 %) showed the highest variation, while Sailershausen (31.4 %) and Harcourt (30.2 %) had the most uniform stem forms.

In the full dataset, the overall mean stem form (SF) differed considerably among seed sources, with Righi (1.52) and L-P-C (1.51) exhibiting the highest mean stem form, while Tortoiseshell Wood (1.10) and Ast Wood (1.18) ranked the lowest. For the Top 5 dataset the mean SF was higher across all seed sources compared to the full dataset, indicating that selecting the best-growing individuals also improves stem form. The ranking of seed sources remained consistent except for a shift in the top two, with L-P-C (1.72), Righi (1.66), and Harcourt (1.62) as the top performers, while Tortoiseshell Wood (1.32) and Ast Wood (1.33) still had the lowest mean scores.

In addition to an overall increase in mean SF, the coefficient of variation (CV %) was consistently lower in the Top 5 subset across all seed sources. This reduction in variability suggests that stem form improves not only in mean ranking but also in consistency when selecting superiorly growing individuals. The most pronounced gains were observed for Tortoiseshell Wood (+0.22) and Stoopers Wood (+0.19), highlighting that while these seed sources ranked lower overall, they contain individuals with potential for stem straightness.

Table 22. Mean for stem form per seed source and coefficient of variation (CV), across all sites for original population (n=1624) and the top 5 trees in each plot (n=540)

Seed Source	Mean SF (Full Dataset)	Mean SF (Top 5 Subset)	CV % (Full Dataset)	CV % (Top 5 Subset)
9 Righi	1.52	1.66	33.5 %	28.6 %
7 L-P-C	1.51	1.72	41.3 %	28.1 %
5 Harcourt	1.46	1.62	30.2 %	26.3 %
4 Escatalens	1.43	1.58	36.2 %	28 %
6 Rahay	1.35	1.50	44.5 %	35.8 %
8 Sailershausen	1.36	1.43	31.4 %	30.4 %
2 Stoopers Wood	1.21	1.40	39.9 %	30.7 %
1 Ast Wood	1.18	1.33	41.7 %	34.3 %
3 Tortoiseshell Wood	1.10	1.32	45.1 %	32.8 %
Mean	1.35	1.51	38.2 %	30.6 %

The stability of rankings in the Top 5 subset, combined with reduced variance, indicates that stem form is strongly influenced by genetic potential. The lack of a significant site × seed source interaction ($p = 0.172$) in the Top 5 dataset further suggests that the best-performing seed sources retain their superior form across different environmental conditions.

Linear mixed model

To account for both fixed and random effects influencing stem form (SF), a linear mixed-effects model was fitted, incorporating site, block, and seed source as random effects. Total height increment after the third growing season *(IHTotal)* was added as a covariate, under the hypothesis that taller trees may develop straighter stems due to stronger apical dominance, while rapid height growth also could result in weaker form due to excessive slenderness.

Model structure

$$SF_{ijk} = \beta_0 + \beta_1(Site_i) + \beta_2(SS_j) + \beta_3(Site_i \times SS_j) + \beta_4(IHTotal) + (1|Block{:}Site) + (1|Site{:}Block{:}SS) + \epsilon_{ijk}$$

LS means for stem form were computed for both the full dataset *(n = 1624)* and the Top 5 subset *(n = 540)*. The rankings observed in the LS means closely aligned with the mean SF values from the descriptive analysis, confirming the genetic differences in stem straightness among seed sources while adjusting for site and height growth effects.

Table 23. Least square means (LS) for stem form per seed source at all sites for original population (n=1624) and the top 5 trees in each plot (n=540)

Seed Source	LS Mean SF (Full Dataset)	LS Mean SF (Top 5 Subset)
9 Righi	1.43	1.62
7 L-P-C	1.43	1.69
5 Harcourt	1.41	1.60
4 Escatalens	1.38	1.57
6 Rahay	1.30	1.49
8 Sailershausen	1.31	1.46
2 Stoopers Wood	1.29	1.42
1 Ast Wood	1.28	1.37
3 Tortoiseshell Wood	1.16	1.34
Mean	1.33	1.51

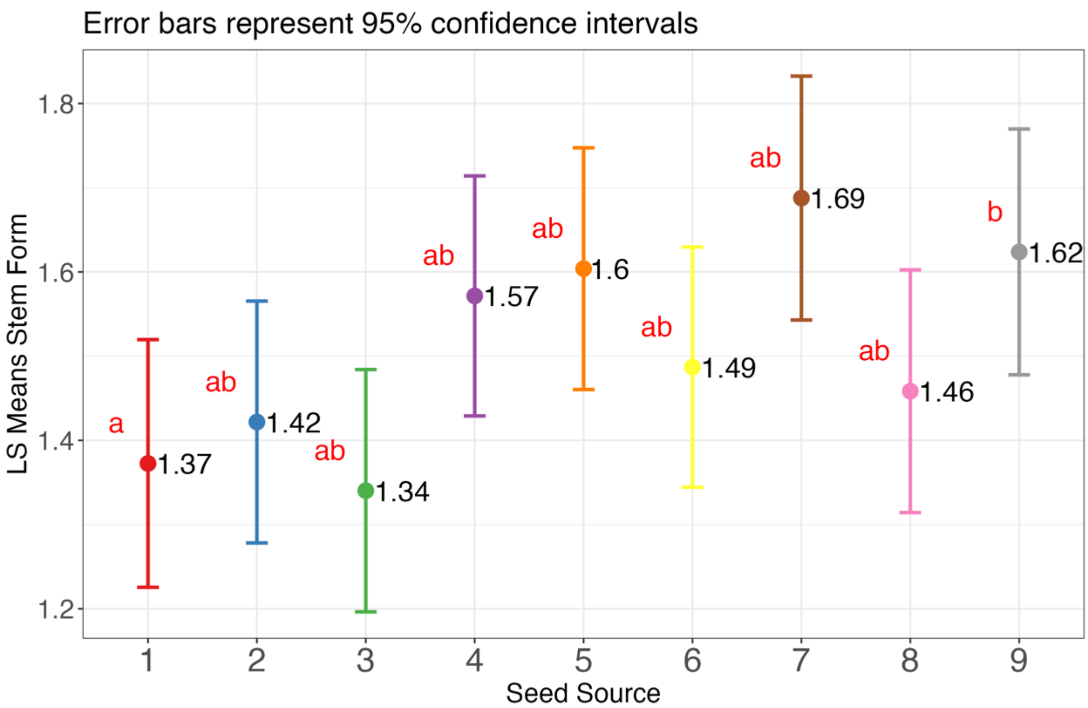

Figure 25. Least square means (LS) for stem form for top 5 trees per plot and seed source at all sites. Site, seed source, and total height increment after the third growing season as independent variables. Stem straight in 0, 1 or 2 planes, or intermediate between these (0.5 and 1.5). Score 2.5 reclassified as class 2. CLD group indicates statistically similar groups based on Tukey's post-hoc test ($p < 0.05$), where seed sources sharing the same letter do not significantly differ. Top 5 trees per plot of original population disregarding beat-ups (n=540).

The inclusion of total height increment as a covariate resulted in slightly lower LS mean SF values compared to the unadjusted means. This suggests that some of the variation in stem form previously attributed to seed source was linked to differences in tree height.

By adjusting for total height increment, the model isolates the genetic component of stem form more effectively, revealing that while taller trees generally develop straighter stems, genetic differences in stem form persist even when height is accounted for. The stability of seed source rankings after this adjustment indicates that stem form is not merely a byproduct of height growth but also reflects inherent genetic traits of each seed source.

Figure 26. Lugny-Plottes-Chardonnay tree at Sotterley with stem form graded as 2.5. 1 February 2023.

Future crop trees

A visual assessment of overall quality and vitality based on growth, stem form, branching, and vigour showed that Sotterley had the largest proportion of certain future crop trees with 13.4 % recorded as having excellent form. Fontmell and Spernal had a significantly lower proportion of trees with the highest rating at 3.7 % and 2.3 % respectively. The difference between Fontmell and Sotterley were not as significant in the second class of trees with 41.7 % and 49.2 % respectively, whereas at Spernal only 23.9 % were graded as trees with good form.

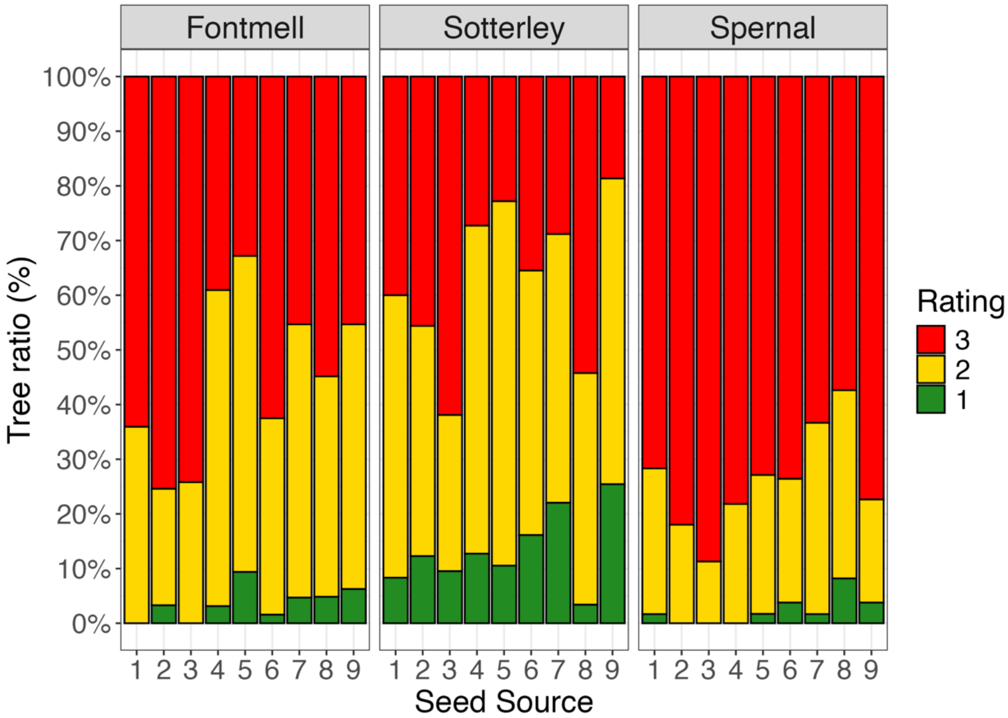

Figure 27. Visual assessment of potential future crop trees per seed source and site. Rating 1= Excellent form, 2=Good form, 3=Poor form, recorded in February 2023. Original population disregarding beat-ups (n=1624).

Table 24. Visual assessment of potential future crop trees per site. Rating 1=Excellent form, 2=Good form, 3=Poor form, recorded in February 2023. Original population disregarding beat-ups(n=1624)

Site	Rating	n	%
Fontmell	1	21	3.7
Fontmell	2	237	41.7
Fontmell	3	311	54.7
Sotterley	1	71	13.4
Sotterley	2	261	49.2
Sotterley	3	199	37.5
Spernal	1	12	2.3
Spernal	2	125	23.9
Spernal	3	387	73.9

Among the seed sources, Righi (11.9 %) and L-P-C (9.3 %) had the largest proportion of trees classified as excellent form, while Tortoiseshell Wood (3. 2 %) and Stoopers Wood (3.3 %) had the lowest across all sites. Harcourt (42.8 %) and Escatalens (47.7 %) had the smallest proportion of trees classified as unsuitable, further supporting their favourable genetic characteristics for stem quality. In contrast, Tortoiseshell Wood (74.9 %) and Stoopers Wood (68.2 %) had the highest proportions of poorly formed trees, making them less desirable for high-value timber production.

Righi and L-P-C had a very high proportion of trees with excellent form at Sotterley with 25 % and 22 % respectively, as well as a high proportion of trees with good form at 56 % and 49 %. Sailershausen had the lowest amount of trees with excellent form at Sotterley with just 3 % and 42 % with good form. However, at Spernal it received the highest ranking in both categories with 8 % of excellent form and 34 % of good form. At Fontmell, Harcourt was the highest graded seed source in the first two categories with 9 % and 58 %.

A two-way ANOVA was performed to assess the effects of seed source, site, and their interaction on future crop tree classification. The results revealed highly significant effects for both seed source ($p < 0.001$) and site ($p < 0.001$), confirming that both genetic and environmental factors influence tree form. Additionally, a significant interaction effect ($p < 0.001$) between seed source and site was detected, confirming that the relative ranking of seed sources was not entirely consistent across sites.

3.7 Branch angle and branch type

Branch angle

Branch angle is a key morphological trait influencing tree architecture and timber quality. A wider branch angle is generally preferred in forestry, as it reduces competition between branches and facilitates better stem form development. Analysis of branch angles across seed sources revealed significant variation, suggesting a strong genetic influence on this trait.

Escatalens exhibited the widest branch angles on average (71.2°), followed closely by Righi (69.6°), Harcourt (68.7°), and L-P-C (68.3°). These values were all above the overall mean of 65°, indicating that these seed sources may have superior architectural properties for timber production. In contrast, Stoopers Wood had the steepest branch angles, averaging 59.5°, followed by Ast Wood (61.8°) and Tortoiseshell Wood (62.1°).

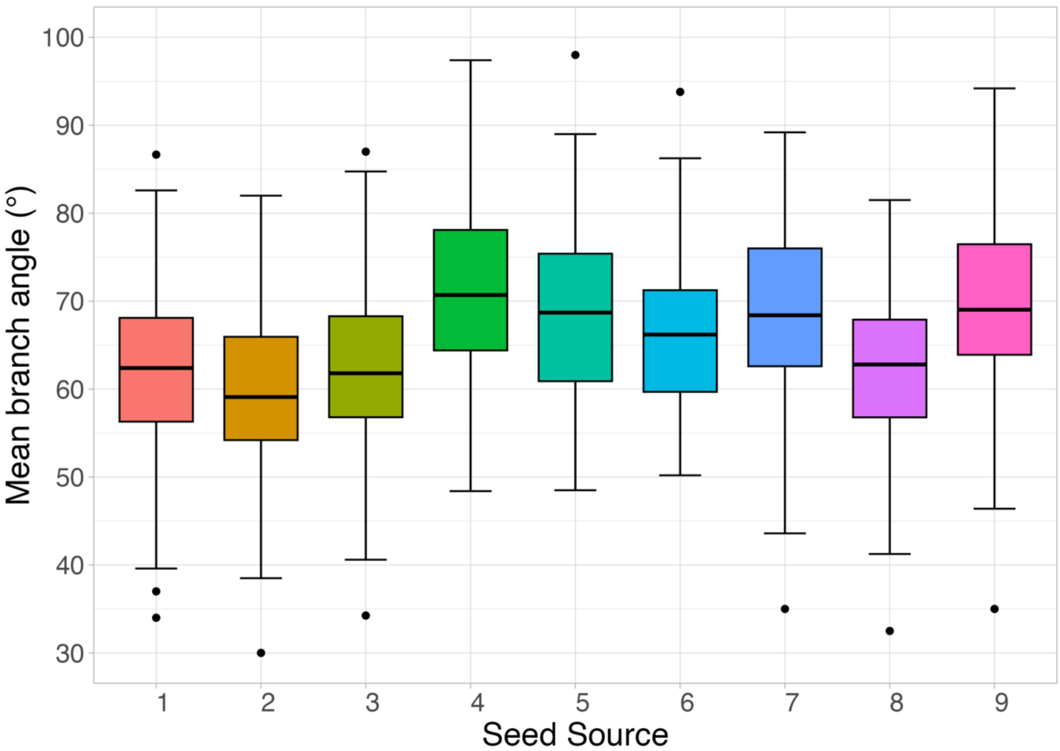

Figure 28. Mean branch angle in degrees (°), per seed source at Fontmell and Sotterley, recorded in February 2023. Original population disregarding beat-ups (n=1100).

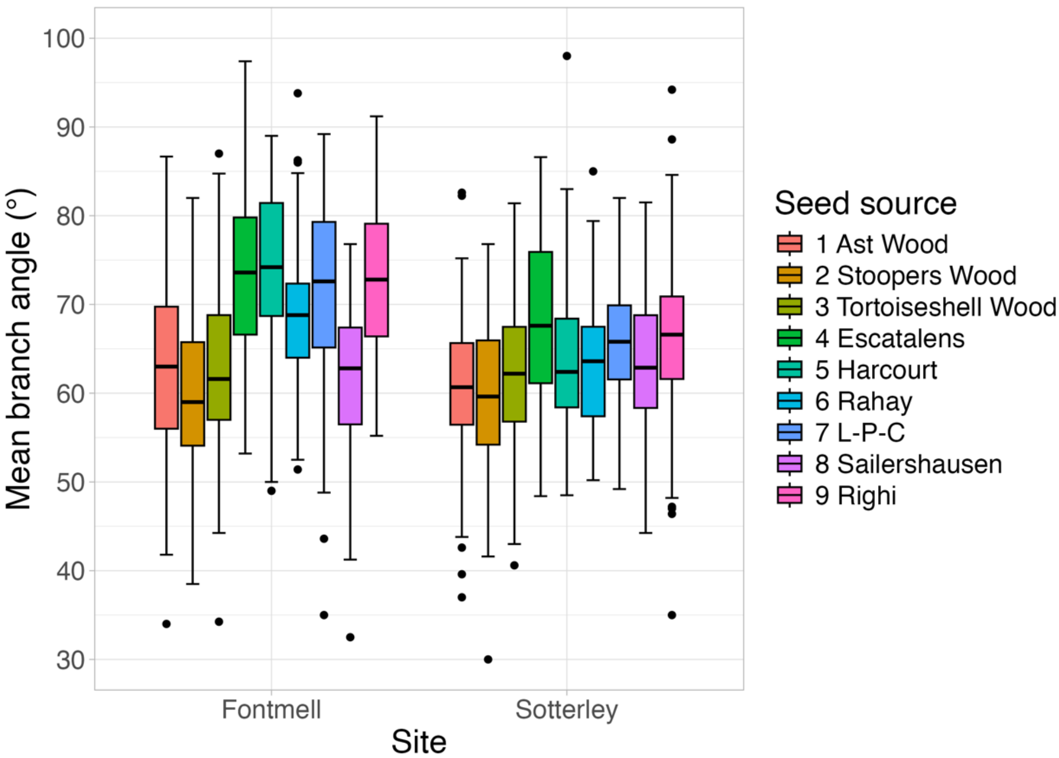

Figure 29. Mean branch angle in degrees (°), per seed source and site (Fontmell and Sotterley), recorded in February 2023. Original population disregarding beat-ups (n=1100).

To assess the effects of seed source, site, and block structure on branch angle, a linear mixed-effects model was applied. The model accounted for both genetic and environmental influences while incorporating total height increment *(IHTotal)* as a covariate to assess its impact on branch angle variation.

Model structure

$$BA_ijk = \beta_0 + \beta_1(Site_i) + \beta_2(SS_j) + \beta_3(Site_i \times SS_j) + \beta_4(IHTotal) + (1|Block{:}Site) + (1|Site{:}Block{:}SS) + \epsilon_ijk$$

The results showed highly significant effects of seed source ($p < 0.001$) and site ($p = 0.008$), as well as a significant interaction ($p < 0.001$), indicating that the performance of different seed sources varied between sites. Variance partitioning revealed that genetic effects accounted for most of the variation (77.2 %), reinforcing the strong heritability of this trait. Site effects explained 6.4 % of the variation, suggesting that local environmental conditions have a minor effect, while block effects contributed an additional 6.4 %, reflecting microsite influences. The inclusion of total height increment *(IHTotal)* as a covariate accounted for 16.4 % of the variance, suggesting that taller trees tend to develop wider branch angles, potentially due to greater light interception and apical dominance.

The LS means confirm that Escatalens and Righi exhibited the widest branch angles, while Stoopers Wood and Ast Wood had the steepest angles, suggesting potential disadvantages for timber production.

Table 25. Least square means (LS Means) for branch angles, across seed sources at Fontmell and Sotterley. Standard errors (SE) and 95% confidence intervals (Lower CL, Upper CL). CLD group indicates statistically similar groups based on Tukey's post-hoc test ($p < 0.05$), where seed sources sharing the same letter do not significantly differ. Recorded in February 2023. Original population disregarding beat-ups (n=1100)

Seed Source	LS Mean Branch Angle (°)	SE	Lower CL	Upper CL	CLD Grouping
4 Escatalens	71.2	1.009	69.2	73.2	a
9 Righi	69.6	0.960	67.6	71.5	ab
5 Harcourt	68.7	0.979	66.7	70.7	ab
7 L-P-C	68.3	0.963	66.4	70.3	ab
6 Rahay	66.4	0.954	64.5	68.3	b
3 Tortoiseshell Wood	62.1	0.954	60.2	64.1	c
8 Sailershausen	61.8	0.967	59.9	63.8	c
1 Ast Wood	61.8	0.957	59.8	63.7	c
2 Stoopers Wood	59.5	0.977	57.5	61.4	c

Note: Groups sharing the same letter are not significantly different at $p < 0.05$.

Branch type

The distribution of branch types varied significantly across seed sources and sites. At Fontmell, Harcourt and Escatalens exhibited the highest proportion of trees with normal branching, accounting for 86 % and 83 %, respectively. Righi and L-P-C followed closely, both at approximately 70 % normal branching. In contrast, Sailershausen displayed the highest proportion of ascending branches, with 50 % of trees exhibiting this growth form. Similarly, Ast Wood and Stoopers Wood had around half of their trees classified as having ascending branches.

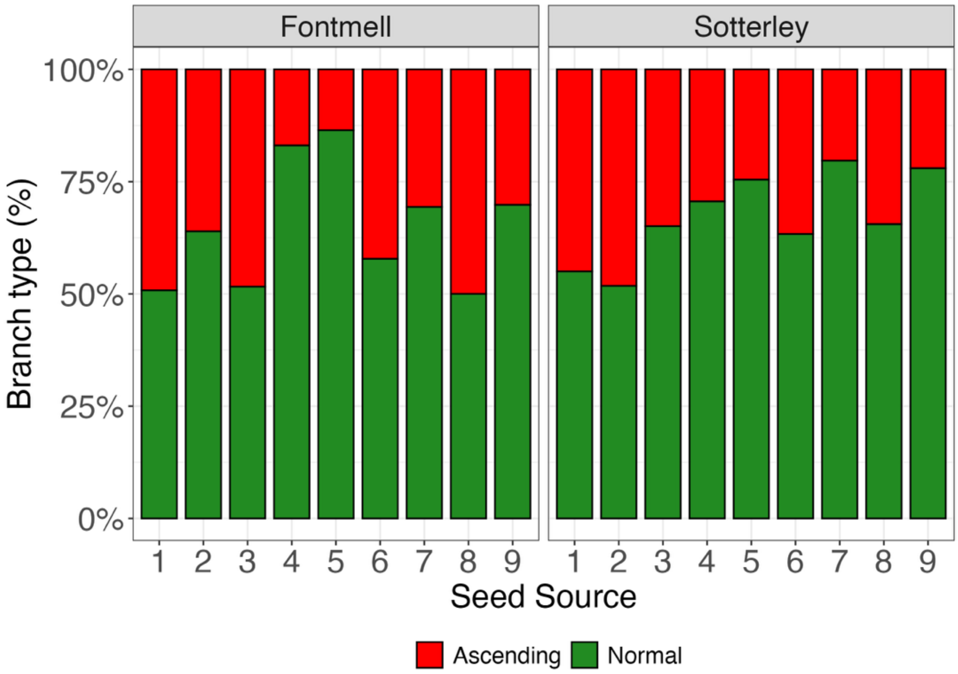

Figure 30. Branch type per seed source at Fontmell and Sotterley, recorded in February 2023. Original population disregarding beat-ups (n=1100).

At Sotterley, a similar pattern emerged, with L-P-C and Righi having the highest proportion of normal branches (80 % and 78 %, respectively), followed by Harcourt (75 %) and Escatalens (71 %). However, Sailershausen had a lower proportion of ascending branches at Sotterley, with 66 % of its trees exhibiting normal branching. Stoopers Wood and Ast Wood had the lowest proportion of normal branches, at 52 % and 51 %, respectively.

A Pearson's Chi-squared test was performed to determine whether there was a significant association between branch type and the combination of seed source and site. The results revealed a highly significant relationship ($\chi^2 = 60.36$, df = 17, $p < 0.001$), leading to the rejection of the null hypothesis. This indicates that branch type distribution is not independent of seed source and site; rather, certain seed sources exhibit a distinct tendency toward normal or ascending branching, and this pattern varies across sites.

3.8 Branch density and pruning requirements

There were noticeable differences in branch density and pruning needs across sites and seed sources. Sotterley, which had the tallest trees on average, exhibited a 19 % higher mean number of branches compared to Fontmell after the third growing season. However, the difference in pruned branches was less pronounced, with 14 % more branches pruned at Sotterley. At Fontmell, 32 % of branches were pruned, compared to 30 % at Sotterley. After the fourth growing season, the difference in total number of branches increased to 24 %, while the number of pruned branches increased by 43 %, reflecting both vigorous branching and slightly higher need for corrective pruning at Sotterley. Spernal had a 12 % lower branch density than Fontmell, but still a higher number of pruned branches, suggesting a greater number of problematic branches.

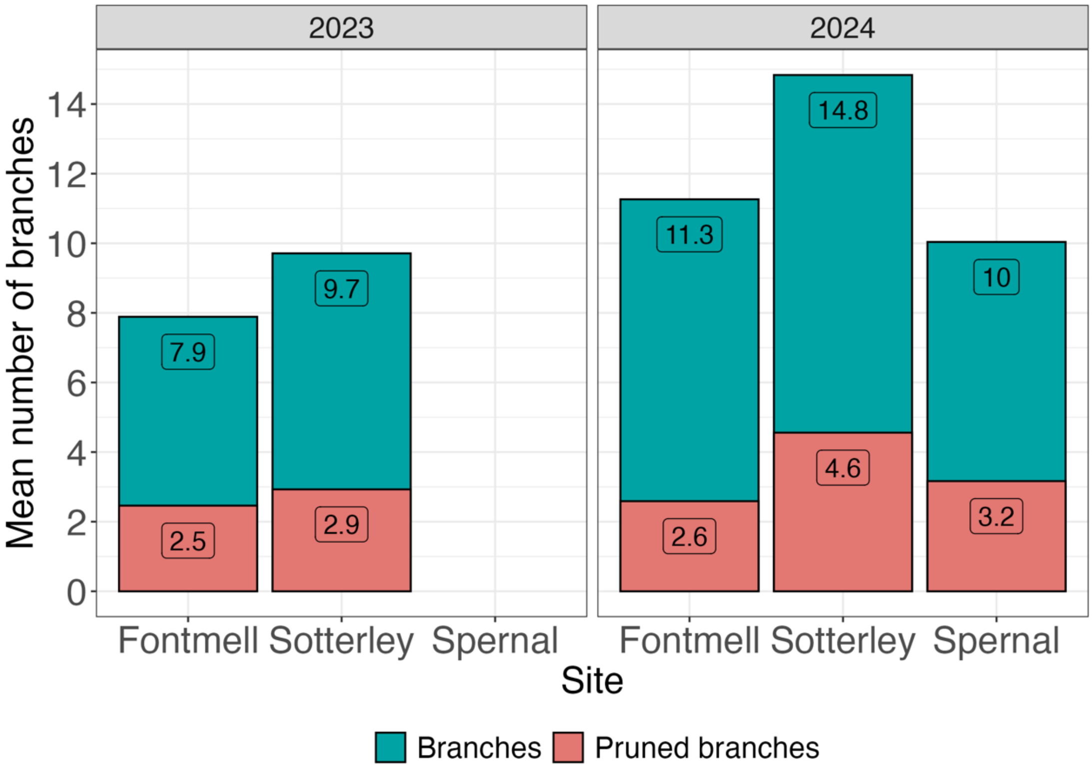

Figure 31. Total mean number of branches and branches pruned, for all seed sources at Fontmell and Sotterley, recorded in February 2023 (n=553), and for all sites in April 2024 (n=816). Original population disregarding beat-ups.

Table 26. Pruning ratio per site after the third and fourth growing season

Site	Pruning ratio 2023	Pruning ratio 2024
Fontmell	31.6 %	23 %
Sotterley	29.9 %	31.1 %
Spernal	No data	32 %

A strong positive correlation was found between total tree height and number of branches in both 2022 ($r = 0.56$, $p < 2.2e-16$) and 2023 ($r = 0.62$, $p < 2.2e-16$), indicating that taller trees generally supported more lateral shoots. This was confirmed by linear regression, where tree height alone explained 32–38 % of the variation in branch number ($R^2 = 0.32–0.38$). Including seed source as a covariate did not significantly improve the model for 2023 but had a small yet significant effect in 2024 ($p = 0.0025$), suggesting a minor genetic influence on branching independent of height.

L-P-C, one of the tallest seed sources on average, had the highest branch density after both the third and fourth growing seasons, with 10.6 and 14.6 on average. Despite this, it was among the seed sources with the lowest average number of branches pruned (2.7 in 2023; 3.7 in 2024), suggesting a favourable branching structure. Righi and Rahay, which also ranked among the tallest, showed similar trends with a moderate number of branches and relatively few requiring pruning. In contrast, Ast Wood — one of the shortest seed sources — had a surprisingly high mean branch density (10.4) and a relatively high number of pruned branches (3.1).

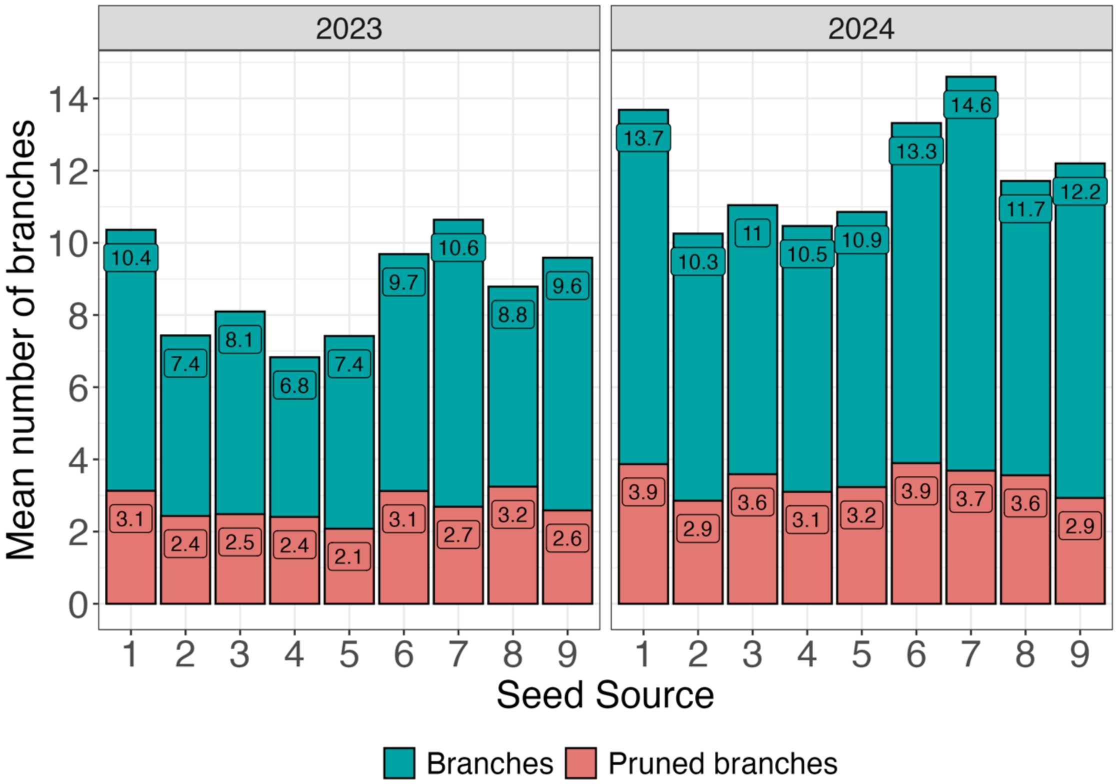

Figure 32. Total mean number of branches and branches pruned, per seed source at Fontmell and Sotterley, recorded in February 2023 (n=553), and for all sites in April 2024 (n=816). Original population disregarding beat-ups.

A low number of pruned branches indicates fewer problematic branches causing inferior stem quality. Righi and L-P-C had the lowest pruning ratio during both growing seasons, despite being the two tallest seed sources on average. Suggesting that these seed sources not only exhibit strong growth but also maintain a more favourable branching structure with fewer defects requiring pruning. Conversely, the English seed sources — with the shortest mean heights — had a high pruning ratio, indicating a higher proportion of problematic branches requiring removal. The overall decreasing pruning ratio at Fontmell and Sotterley after the fourth growing season could be due to the removal of problematic branches in the previous year.

Table 27. Pruning ratio (%) per seed source at Fontmell and Sotterley, recorded in February 2023 (n=553), and for all sites in April 2024 (n=816). Original population disregarding beat-ups

Seed Source	Pruning ratio 2023 (%)	Pruning ratio 2024 (%)
1 Ast Wood	33.3	28.6
2 Stoopers Wood	32.4	26.9
3 Tortoiseshell Wood	30.9	31.5
4 Escatalens	34.3	30
5 Harcourt	27.6	28.8
6 Rahay	31.6	27.8
7 L-P-C	25.5	23.8
8 Sailershausen	36.4	27.6
9 Righi	26	22.1
Mean	30.9	27.5

Pruning type

The distribution of pruning types provides insight into the severity and nature of crown defects among seed sources. Pruning type 1, which mainly involves the removal of scattered thick or ascending branches in the crown, represents the least problematic scenario and was the most common intervention across all seed sources after the third growing season.

L-P-C and Harcourt stood out with the highest share of pruning type 1, exceeding 91 %, suggesting a relatively clean crown architecture with minimal defects. In contrast, Escatalens and Sailershausen had a significantly higher proportion of more severe pruning types. Only around 75 % of trees in these seed sources were classified as type 1, while the remainder required the removal of a fork (2), or even multiple problematic branches including forks and double stems (types 3–5) with an almost equal share at Fontmell and Sotterley. This indicates a more complex crown structure prone to forking and structural instability.

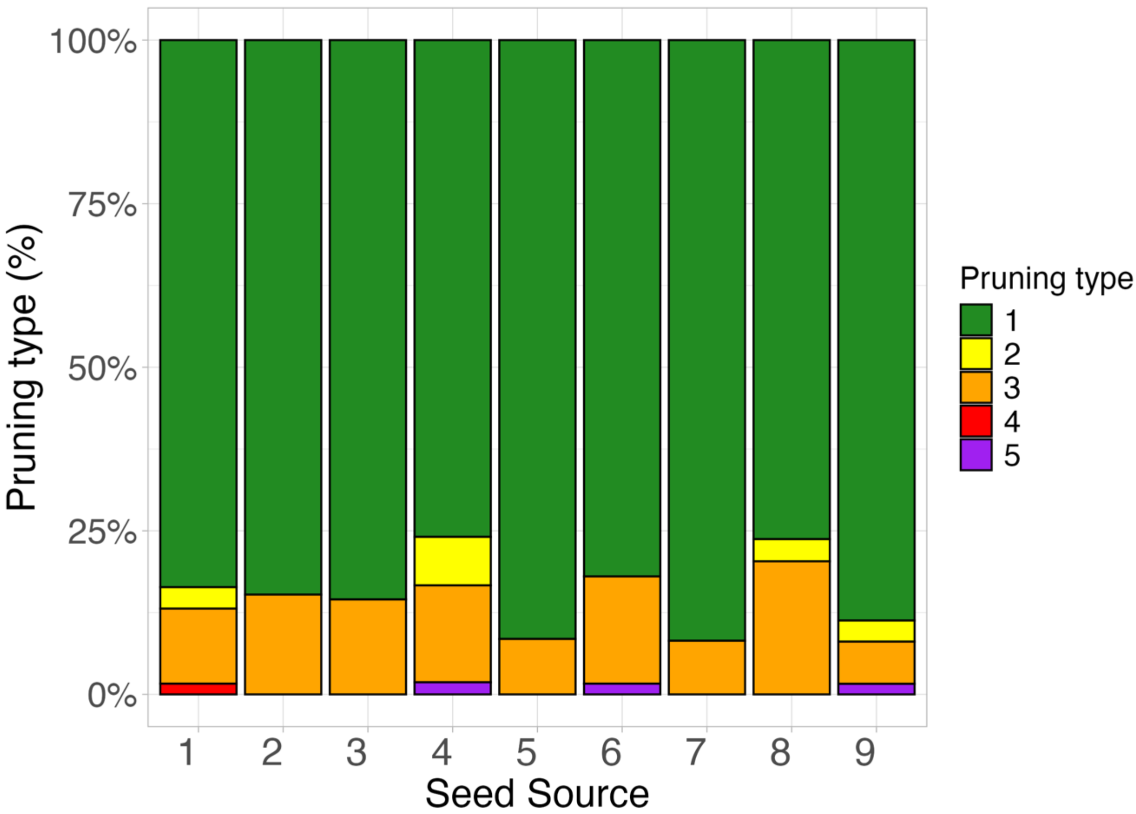

Figure 33. Pruning type per seed source at Fontmell and Sotterley. Pruning types; 1 = Scattered in crown, 2 = One fork pruned, 3 = Fork pruned, and one or more additional branches pruned, 4 = singling of double stem, 5 = singling of double stem and one or more additional branches pruned. Recorded in February 2023, original population disregarding beat-ups (n=553).

After the fourth growing season, fewer trees required corrective pruning overall, and the frequency of more severe pruning types decreased markedly — likely due to effective interventions in the previous year. Fork-related pruning types (2 and 3) were still present, however, particularly among certain seed sources. Sailershausen had the highest combined proportion of fork-pruned trees (22 %), followed by Righi (16 %) and L-P-C (15 %). In contrast, Harcourt (7 %) and Tortoiseshell Wood (5 %) showed the lowest frequencies of problematic pruning. This trend may also reflect delayed pruning at Spernal, where many trees were previously too small for intervention, potentially leading to the accumulation of structural defects.

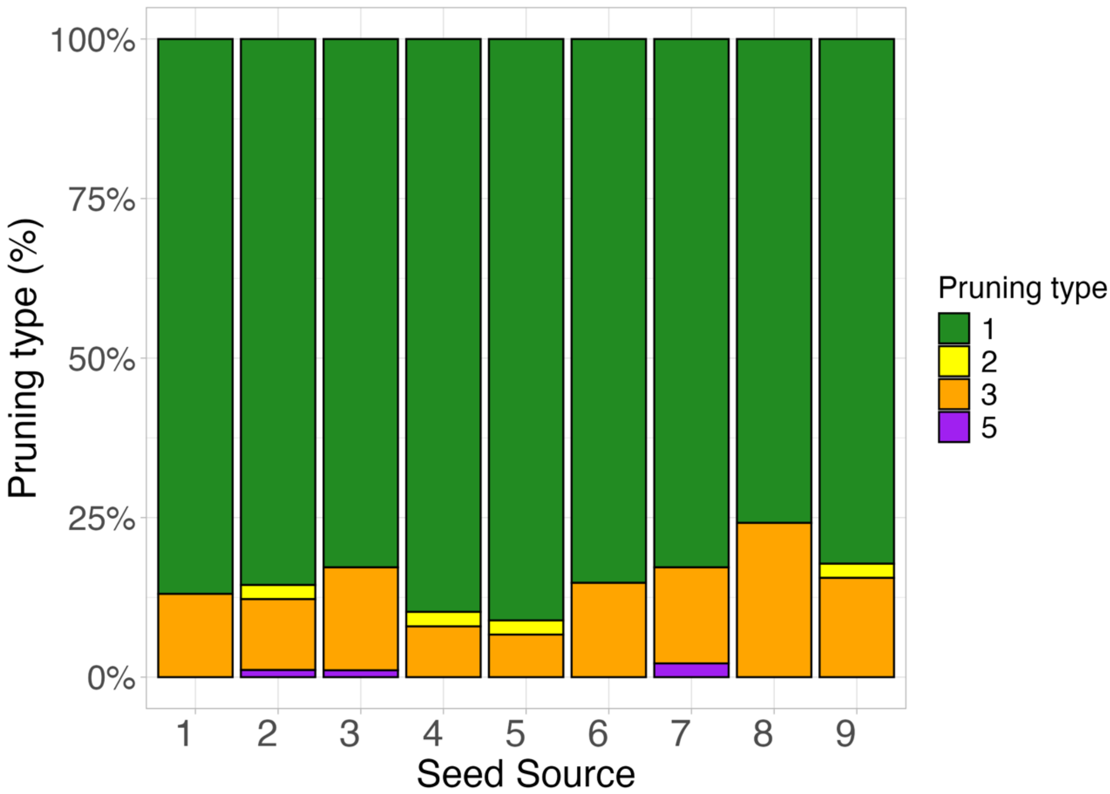

Figure 34. Pruning type per seed source at all sites. Pruning types; 1 = Scattered in crown, 2 = One fork pruned, 3 = Fork pruned, and one or more additional branches pruned, 4 = singling of double stem, 5 = singling of double stem and one or more additional branches pruned. Recorded in April 2024, original population disregarding beat-ups (n=816).

Correlation between crown architecture and height growth

A Spearman correlation analysis showed weak to moderate associations between crown traits recorded in 2023 and height increment in the following growing season (2024). The number of branches had a weak positive correlation with subsequent height growth ($\rho = 0.119$), while the number of pruned branches showed a slightly stronger correlation ($\rho = 0.197$). A moderate correlation between total and pruned branches was also observed ($\rho = 0.438$), suggesting that trees with more branches also tended to require more interventions.

3.9 Spring and autumn phenology

The phenological stages were assessed using a standardized scale ranging from 0 (dormant) to 9 (fully developed leaves). This system follows the phenology monitoring protocol for wild service tree by Skovsgaard (2015, Appendix 2). The same approach was used for autumn dormancy assessments, where stage 9 represents fully developed leaves, and stage 0 represents complete dormancy

(Appendix 3). The timing of bud burst, and leaf expansion is crucial, as late frost events can damage young leaves, affecting growth and survival. Autumn dormancy is equally important, as late-growing trees may be exposed to early frosts, potentially causing dieback. The dots in the figures represent raw data points collected in the field, while the trend lines show smoothed LOESS regressions, capturing overall phenology progression.

Spring bud burst and leaf flush

There was a rather large variation in leaf flush among the seed sources *(Fig. 35)*. Righi had the earliest bud break and was also the first seed source to have fully developed leaves on the 11th of May. It was shortly followed by Sailershausen, Escatalens, and L-P-C. Harcourt and Rahay was fully developed about a week later, while the English seed sources were not fully developed until over two weeks after Righi.

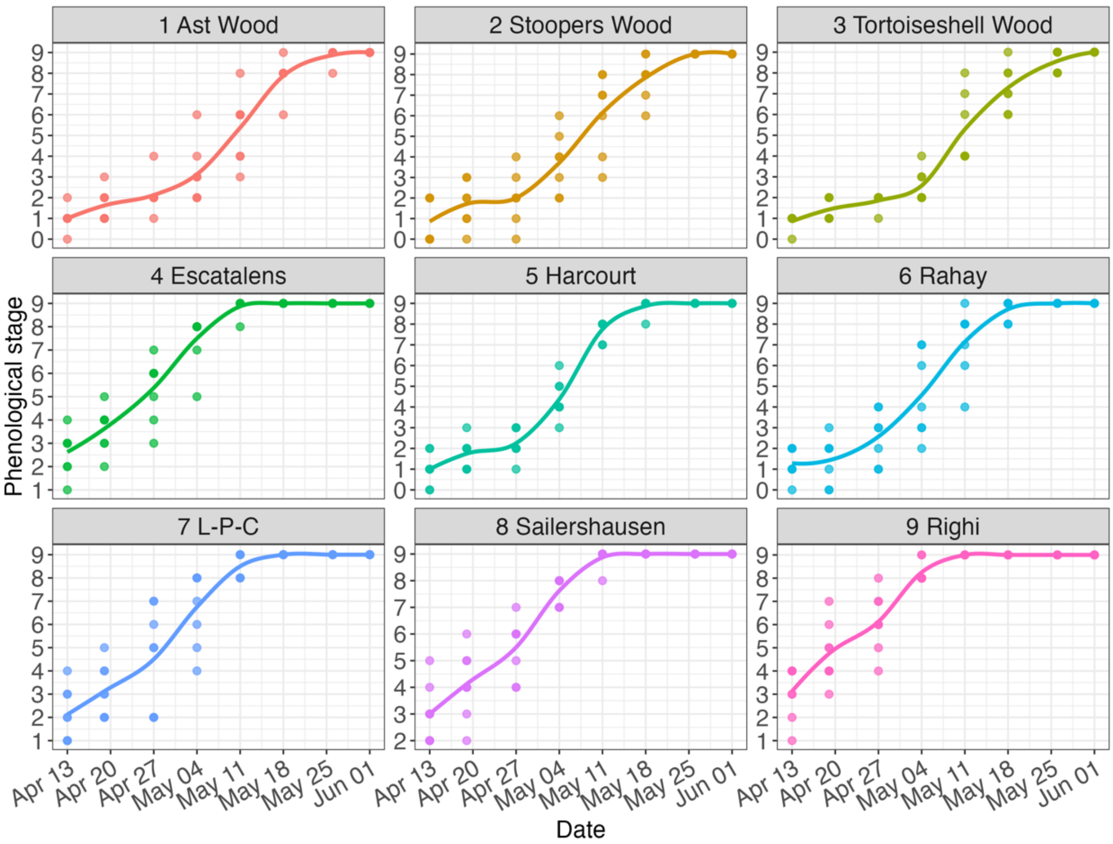

Figure 35. Leaf flush stage (0-9) of wild service trees studied at the Spernal site in spring 2023 (n=69). Each point represents an individual observation, regression trend lines illustrate the overall dormancy progress.

Spring apical shoot increment

Righi also exhibited the highest mean apical shoot increment, reaching an average of 45 cm at the final measurement on June 1st *(Fig. 36)*. Despite its late development, Stoopers Wood had the second highest mean height increment with an average of 40 cm. All seed sources had a mean height increment of over 30 cm by the last spring measurement. By the end of the growing season (September 25), Righi maintained the highest mean height increment (47.1 cm), while the highest individual increment was recorded for Rahay (84 cm). The decline in increment for some of the seed sources in *Fig. 36* are due to broken tops and apical shoot dieback.

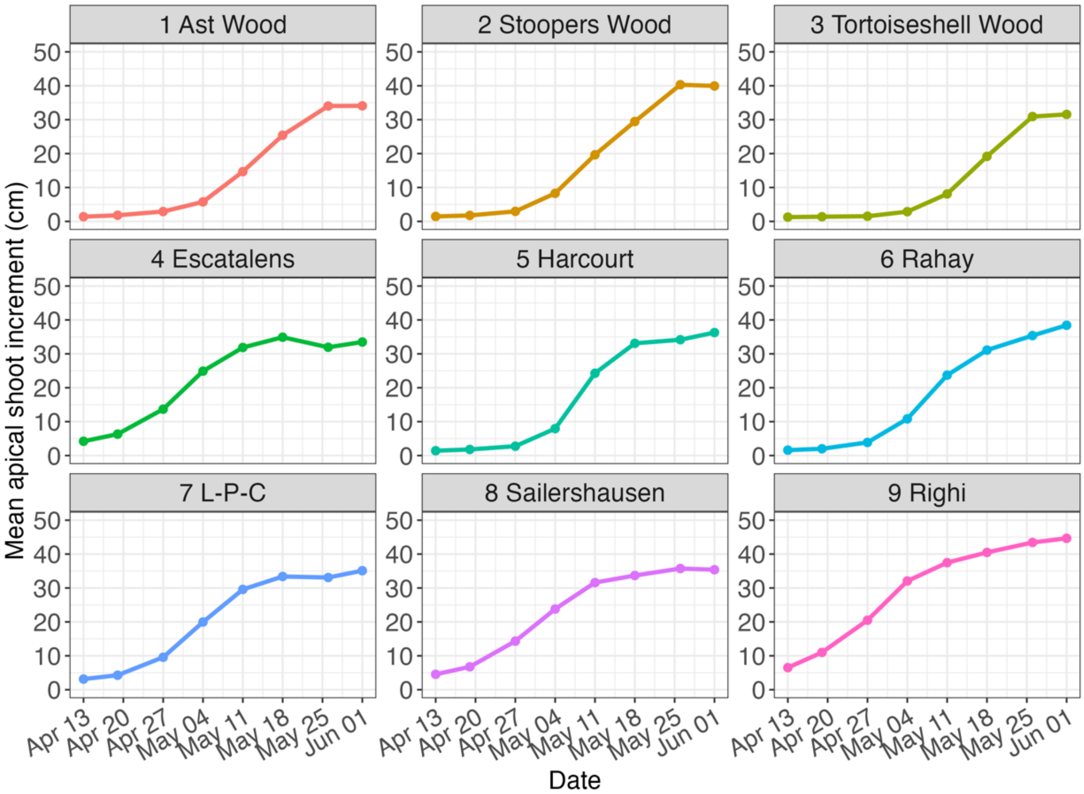

Figure 36. Mean apical shoot increment (cm) of wild service trees studied at the Spernal site in spring 2023 (n=69). The decline in increment for some of the seed sources are due to broken tops and apical shoot dieback.

Table 28. Wild service trees studied at the Spernal site in spring 2023 (n=69). H_3 =Mean height after third growing season, I_{H4} =Mean apical shoot increment from April 13 – 1 June, H_4 =Mean height on 1 June 2023

Seed source	H_3 (cm)	I_{H4} (cm)	H_4 (cm)	Best individual increment (cm)
1 Ast Wood	104.5	34.1	138.6	45
2 Stoopers Wood	127.6	39.9	167.5	49
3 Tortoiseshell Wood	104.9	31.6	136.5	60
4 Escatalens	99.9	33.5	133.4	75
5 Harcourt	99.4	36.3	135.7	71
6 Rahay	110.6	38.4	149	84
7 L-P-C	128.4	35.1	163.5	59
8 Sailershausen	115.1	35.9	151	72
9 Righi	119.5	44.7	164.2	67
Mean	112.2	36.6	148.8	64.7

During the data collection in April 2024, photos were taken of each plot at each site and a visual assessment grading of the spring flush was performed based on the photographs. A similar pattern as the one seen in the Spernal spring phenology study could be seen for all sites with an earlier flush noted for the continental seed sources.

Autumn phenology and dormancy progress

A similar pattern was observed in autumn phenology, where the continental seed sources exhibited a longer growing season. Rahay, Righi, L-P-C, and Sailershausen were the last seed sources to enter dormancy with some of the trees still flushing on December 1st. The first light frost occurred in mid-October, which may explain the rapid acceleration of the dormancy process seen in the graph. No evident frost damage was seen during the study.

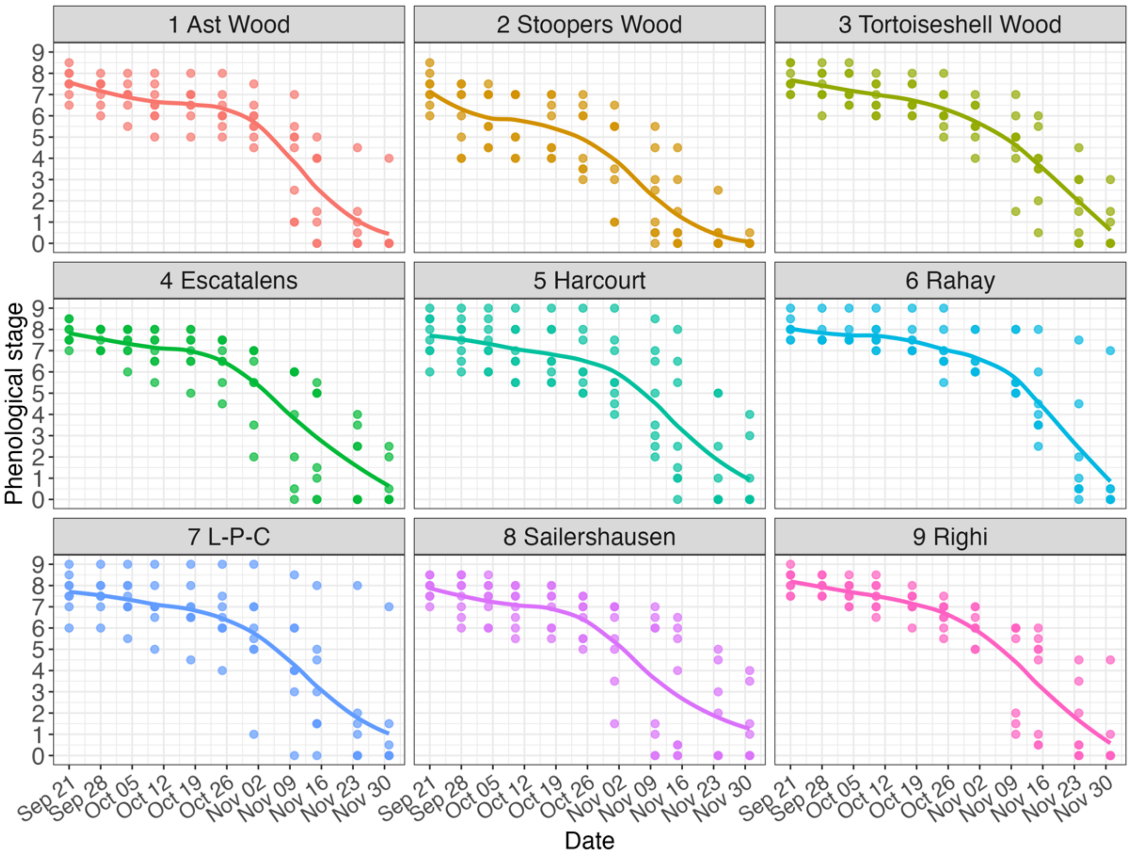

Figure 37. Dormancy stage (0-9) of wild service trees studied at the Spernal site in autumn 2023 two trees in each plot (n=72). Each point represents an individual observation, regression trend lines illustrate the overall dormancy progress.

4. Discussion

This study provides an early evaluation of a field trial testing nine seed sources of wild service tree, planted across three sites in southern England. After four growing seasons, clear differences in growth, stem quality, and branching structure were observed among seed sources and across sites. These findings contribute to the growing body of research on minor broadleaved species with potential for high-quality timber production, particularly in the context of climate change, and diversification in European forestry.

Site effects on survival and growth performance

Noticeable variations in growth and survival were observed across sites, highlighting the importance of environmental conditions as well as site preparation and maintenance. Fontmell had the highest survival rate, and an overall more uniform stand development, with a high survival rate and better growth among the admixed species. The wild service trees at Sotterley showed superior growth performance during the first growing seasons, although with a lower survival rate and more struggling admixed species. Spernal had the lowest survival rate and height increment, with the admixed species struggling even more than at Sotterley. These trends were consistent with variation in site conditions and soil structure, as well as an effect of site preparation and maintenance.

The favourable establishment at Fontmell likely resulted from its well-aerated calcareous brown earth soil with high sand content (50 %) and higher precipitation during the first growing season. The successful establishment of triticale as a cover crop, helped suppress weeds and likely provided shade during the critical first growing season, which was very dry in May. Despite the preference of south-facing slopes at this latitude, the northwest facing slope was likely beneficial during the droughts occurring in the first and third growing season. The location at the lower end of a slope also provided flowing groundwater, this combined with a more sheltered site, resulted in more stable soil moisture conditions.

The site at Sotterley showed significantly higher mean height and growth rates among all seed sources during the first two growing seasons, with Fontmell catching up in the third and fourth growing season. The south-facing slope and well-drained soil with a higher clay content seemed to provide good growing conditions.

Although being the driest site with failed establishment of triticale, extensive subsoiling and mole draining, coupled with consistent irrigation and the use of straw mulch, likely enhanced water retention and root development. The very dry conditions were represented by a lower survival rate among wild service trees, as well as the substantial loss, and stalled growth of the admixed species.

Spernal presented the most challenging conditions, with compacted surface water gley soil, flat topography, and high silt content impeding both aeration and drainage. The lack of site preparation combined with failed triticale establishment, caused extensive weed growth—intensifying drought stress and competition despite high volumes of irrigation. The result was significantly reduced survival and growth, particularly among admixed species, reinforcing the importance of site selection- and preparation, as well as maintaining competing vegetation. The fluctuation in soil moisture and strong competition likely also caused the higher occurrence of apical shoot dieback.

These patterns underscore the critical role of site conditions, drainage, and early maintenance in determining establishment success and growth potential. They also reinforce the importance of evaluating genetic performance within the context of specific site environments.

The linear mixed-effects model provided a deeper understanding of how both environmental and genetic factors influence height increment in young wild service trees. The model revealed that seed source had a significant effect across both the full dataset and the subset of the top 5 trees per plot, confirming that seed source selection plays a vital role in early growth potential.

Environmental variables were also highly influential. Soil fertility, represented by cation exchange capacity (CEC), and water availability during April-August (W5: precipitation and irrigation), were both strong predictors of height increment. A significant interaction between W5 and CEC suggests that trees growing in more fertile soils utilised water more efficiently, reinforcing the synergy between nutrient supply and moisture availability. This provides quantitative support for the observed advantages at Fontmell and Sotterley, where soil amelioration improved both drainage and resource availability.

Initial seedling height at planting also emerged as a key predictor, but its effect varied across seed sources. The significant interaction between seed source and initial height indicates that taller seedlings provided a growth advantage in some seed sources more than others, possibly due to early apical dominance or root system development.

The carbon-to-nitrogen ratio (C:N) showed significance only in the full dataset, suggesting that its effect may be more pronounced in slower-growing or more variable individuals. Overall, the model illustrates the multifactorial nature of early height development, shaped by genetic potential, site fertility, water access, and initial plant characteristics. Yet, it is important to note that while the model accounted for key environmental variables, it did not explicitly incorporate factors such as topographic position, ground vegetation competition, and microclimatic effects—elements that clearly influenced performance, as seen in the contrast between sites.

Seed source performance and genetic considerations

The seed sources in this study can be broadly grouped into three performance categories based on growth, stem form, branching characteristics, and overall vitality. Among the top-performing sources were the Italian Righi and the French Lugny–Plottes–Chardonnay (L-P-C), both originating from local woodlands. These two seed sources consistently ranked highest across growth and quality traits. The trees exhibited vigorous height development, wide branch angles, and a relatively low incidence of forking — attributes desirable for high-quality timber production. Despite late delivery to the nursery, both Righi and L-P-C also had a high germination success, suggesting robust seed viability and overall adaptability. Their superior performance across all sites, reinforces their strong genetic potential and highlights their promise for future deployment in southern England and climatically similar regions.

Escatalens, Harcourt, and Rahay — all originating from French seed orchards — formed a second group of well-performing seed sources. While their height growth was slightly lower than that of Righi and L-P-C, they showed consistent performance across sites and particularly excelled in stem form and branch structure. Escatalens, for example, exhibited fine branching structure, with the widest average branch angles of all seed sources. Harcourt had among the lowest proportion of poorly formed trees, suggesting strong phenotypic stability and quality. This reliable performance underscores the importance of controlled selection in provenance trials and confirms these seed sources potential for high-quality timber production under English conditions.

Sailershausen displayed more variable results. While its growth performance was solid, it exhibited greater internal variability, and a higher frequency of dieback, ascending branches and forked stems. This may reflect a broader genetic base due to the inclusion of more parent trees. Notably, Sailershausen performed well in the Liliental provenance trial in southern Germany, a site that — like Sotterley and Spernal — experiences low annual precipitation (600–700 mm). This historical context suggests that Sailershausen may perform well over longer rotations or under continued drought pressure, even if its early performance is more variable.

The three English seed sources — Ast Wood, Stoopers Wood, and Tortoiseshell Wood — generally ranked lower across most growth and quality traits, exhibiting lower height increments, steeper branch angles, and higher rates of apical shoot dieback and forking. However, by the fourth growing season, their growth trajectories began to improve. These seed sources should be more adapted to British conditions but likely require longer rotations to realise their potential. Among them, Stoopers Wood exhibited the best growth rate and most consistent stem form.

When compared to data from the Liliental provenance trial in Baden-Württemberg, the growth performance in this study appears strong. In Liliental, most provenances reached just under two metres in mean height after four growing seasons (Schüte, 2000). In this study, Sailershausen reached 180.8 cm in mean height at Sotterley, and 155.7 cm at Fontmell. Even more notably, Righi and L-P-C exceeded 180 cm at Fontmell and approached 200 cm at Sotterley. This despite the though start, with some of the driest years on record in this region. These results suggest that the mild, temperate climate of southern England — in combination with targeted site preparation may provide highly favourable conditions for certain origins of wild service tree.

Apical shoot dieback and forking

Apical shoot dieback and the development of forks were among the most significant quality-limiting issues observed in the trial. Both traits were likely associated with environmental stress, particularly during the first and third growing seasons, which were marked by drought conditions during the critical leaf-flush and early elongation period. The number of trees affected by apical shoot dieback decreased steadily over time, indicating successful establishment and a reduction in stress sensitivity.

Spernal, which experienced poor drainage in winter and drought in summer, suffered from the highest occurrence of apical shoot dieback and forks. Over the full trial period, almost half of the trees at Spernal had dieback recorded in at least one year, compared to less than a quarter of the trees at Fontmell and Sotterley. These figures highlight not only the harsher environmental conditions at Spernal but also the long-term impact of early site stress on crown development and leader stability.

Among seed sources, Righi, L-P-C, and Harcourt had the lowest incidence of forking and the most consistent apical dominance, reinforcing their suitability for timber production. In contrast, Sailershausen and the English seed sources exhibited a higher rate of ascending branch patterns and forked trees, often in association with apical shoot dieback, traits which may be either genetically encoded or reflect a higher sensitivity to site-level stress. However, the English seed sources had a steady annual decrease of dieback.

The occurrence of forking was significantly higher among trees that had previously suffered apical shoot dieback, and a highly significant correlation between these two traits was confirmed by Chi-squared analysis. Trees that had lost apical dominance early were more than twice as likely to fork, supporting earlier findings that damage to the leader shoot — whether through drought, frost, or mechanical stress — is a primary cause of crown defects (Pietzarka, Lehmann and Roloff, 2009).

While the literature suggests that proleptic growth, increases the risk of frost damage (Eschrich, 1995; Schulz, 1999), this pattern was not clearly observed in this study. In fact, the seed sources with presumably longer growing seasons—such as Righi and L-P-C—showed some of the lowest frequencies of apical shoot dieback and forking. Conversely, English seed sources which were later to flush, and earlier to enter dormancy, exhibited higher rates of dieback, particularly at Spernal which suffered from more environmental stress. This indicates that drought exposure, weed competition, and soil structure may have had a stronger influence on apical shoot dieback than flushing phenology and frost damage. These results highlight the complexity of interacting factors during establishment and point to the value of combining phenological knowledge with field data when evaluating performance.

These findings reinforce the need for proactive site management during establishment, especially in dry years. Site preparation and effective weed control during the first two years could substantially reduce apical dieback and forking. Additionally, seed source selection plays a critical role in resilience, with certain seed sources displaying low dieback and forking across all sites. These traits are essential when selecting material for high-quality timber production.

Diameter growth and branch thickness

In addition to height development, traits such as (DBH) and (DTB) offer valuable insights into seed source vigour and structural development. Seed sources that performed well in height — notably Righi, L-P-C, and Sailershausen — generally also exhibited greater stem diameter and branch thickness, suggesting a shared underlying vigour and resource allocation strategy. An exception was Tortoiseshell Wood, which despite ranking among the shortest seed sources in height, displayed comparatively thick branches. This may indicate a less efficient or more sprawling growth pattern, potentially requiring more corrective pruning. Meanwhile, Escatalens, though modest in height, maintained thin branches and wide branch angles — a combination suggesting good form with minimal intervention.

Branch thickness can reflect overall shoot vigour but also has implications for silvicultural workload. Coarse branching may increase the need for corrective pruning, while finer, well-angled branches may contribute to better natural form. This underscores the importance of not only evaluating growth rates but also considering crown architecture and its management implications when selecting material for timber production.

Together, the DBH and DTB findings reinforce the value of integrating both vigour and form in selection decisions. Seed sources such as Righi and L-P-C combine strong apical growth with moderate branch diameter, while seed sources like Escatalens demonstrate how finer branching traits may also contribute to high timber potential through improved form and reduced pruning demand.

Nursery and site effects on stem form

Stem form is a key determinant of timber quality and commercial value. The trial revealed clear differences in stem straightness among seed sources and between sites, highlighting both genetic and site-specific environmental effects. A nursery effect was also evident — most notably, the frequent occurrence of stems with a spiralling base that then straightened into otherwise well-formed trees. This appeared almost exclusively in the French and Italian seed sources, particularly Righi and L-P-C, while being rare among the English seed sources and Sailershausen.

The likely explanation relates to nursery propagation timing. Due to late seed delivery, the French and Italian seed sources (Escatalens, Harcourt, Rahay, L-P-C, and Righi) were sown in early June, whereas the English seed sources and Sailershausen were sown in late March. The late-sown seedlings had less time to develop robust, upright shoots before the end of the growing season. This may have led to elongation or curvature in response to light conditions, resulting in the spiralling base. However, since these trees typically straightened well above the protective tube, this likely reflects a nursery artefact rather than a genetic flaw.

Site conditions also had a significant effect on stem form. Sotterley had the highest proportion of trees in the top three stem form classes (1.5, 2, and 2.5), followed by Fontmell. This aligns with these sites' well-drained soils, gentle slopes, robust site preparation, and efficient weed control — all contributing to stable growth and apical dominance. In contrast, Spernal had the lowest average stem form, consistent with compacted soils, poor drainage, and a lack of site preparation, which led to intense early weed competition.

These findings highlight how early establishment conditions, both in the nursery and on-site, can strongly influence stem development.

Seed source effect on stem form

Despite the influence of nursery and site effects, stem form was also strongly controlled by genetic factors. Significant differences between seed sources were observed in both the full dataset and the Top 5 subset. The relative ranking of seed sources remained largely consistent in both datasets, reinforcing the conclusion that differences in stem form reflect stable genetic traits rather than random or site-specific variation. Righi, L-P-C, and Harcourt exhibited the best mean stem form across all sites. These seed sources combined good growth with desirable stem form and relatively low variation, making them strong candidates for use in high-quality timber production. Escatalens also performed well, with a strong mean stem form and good consistency across sites.

Rahay and Sailershausen showed moderate stem form values. While their performance was overall good, their stem form was less remarkable than that of the top performers. This result is somewhat surprising for Sailershausen, which was the top-ranked seed source in the Liliental trial in southern Germany (Šeho *et al.,* 2018). However, Sailershausen did show the best stem form at Spernal, with over 60 % of trees in the top three classes.

Among the English seed sources, Ast Wood and Tortoiseshell Wood had the lowest stem form scores and the greatest variability. Stoopers Wood showed clear improvement in the Top 5 subset, suggesting that even within weaker seed sources, superior individuals exist. This underlines the potential of selective propagation and long-term selection strategies for improving timber quality from local material.

The linear mixed-effects model, which included total height increment as a covariate, confirmed that genetic differences in stem form persist even when accounting for tree size. While taller trees tend to exhibit better form, the consistent rankings and model-adjusted means suggest that inherent architectural traits are under strong genetic control.

Future crop trees

The classification of future crop trees provided a more integrative assessment of timber potential by combining growth and form traits. Despite the young age of the trial, meaningful patterns emerged across seed sources and sites. The seed sources that performed best in stem form and height — Righi, L-P-C, and Harcourt — also had the highest proportions of certain future crop trees. These results reinforce the value of combining both vigour and stem architecture when selecting individuals for future silvicultural attention.

Site conditions played a crucial role in shaping future crop tree potential. Well-managed sites with favourable soil structure and moisture availability, such as Sotterley, provided optimal conditions for expressing genetic potential, while more challenging sites, like Spernal, revealed contrasts in adaptability among seed sources. Some sources demonstrated stable quality across environments, while others showed more site-dependent performance, highlighting the importance of genotype-by-environment interactions.

Escatalens, Harcourt, and Rahay derived from French seed orchards, generally displayed a high proportion of well-formed individuals and few structural defects. This may reflect both the selection history of the seed material and a good match between their genetic background and the trial environments. Meanwhile, seed sources of British origin often exhibited a higher proportion of poorly formed trees, though individual variation suggests potential for improvement through within-source selection.

Although the classification is based on a relatively early assessment, these results provide valuable insights for future management. The combination of good form and height growth makes Righi and L-P-C particularly promising for timber-focused planting. Harcourt, Escatalens, and Rahay offer strong alternatives. As the trees mature, these trends will need to be re-evaluated, but the current patterns already offer a solid foundation for early selection and future breeding efforts.

Crown architecture and pruning implications

Crown architecture plays a central role in the future value and management intensity of broadleaved timber species. Traits such as branch angle, branch type, and branch density influence stem form, apical dominance, and the extent of pruning required to produce high-quality timber. Clear differences were observed between seed sources in all these crown traits, and their silvicultural implications are already evident at this early stage.

Branch angle, a key determinant of crown shape and stem straightness, varied significantly among seed sources. Wider angles are generally preferred, as they reduce the risk of forking and facilitate more stable vertical growth. Escatalens, Righi, Harcourt, and L-P-C had the widest mean branch angles, all above the trial average of 65°, with Escatalens leading at 71.2°. These seed sources also performed well in stem form and future crop tree selection, suggesting a positive link between crown architecture and overall timber potential.

In contrast, Stoopers Wood, Ast Wood, and Tortoiseshell Wood showed the steepest branch angles, averaging under 63°, aligning with their lower stem form ratings and higher frequency of forking. These narrow-angled crowns may require more corrective pruning to guide vertical growth and improve stem quality.

Branch type also varied by seed source and was strongly associated with site. Seed sources with steeper angles typically showed a higher share of ascending branches, while those with wider angles had a greater proportion of normal (horizontal to gently ascending) branches. A Pearson's Chi-squared test confirmed a significant association between branch type and the combined effects of seed source and site ($p < 0.001$), indicating both genetic and environmental control.

Branch density and pruning requirements varied significantly among sites and seed sources, further reflecting both environmental and genetic influences on crown structure. As expected, tree height was positively correlated with the number of branches (Pearson's $r = 0.56$–0.62), and regression analysis confirmed that tree height was a significant predictor of branch number in both 2023 and 2024 ($p < 2.2e\text{-}16$). This suggests that taller trees naturally support more lateral growth, likely due to greater shoot vigour and increased light capture.

Sotterley, which consistently had the tallest trees, also exhibited the highest branch densities. However, the higher branch count did not necessarily translate to more problematic branching. In fact, while Sotterley had the highest number of pruned branches in 2024, it also maintained a relatively moderate pruning ratio, reflecting a good balance between vigorous growth and manageable form.

Spernal, in contrast, had a lower average number of branches, likely due to site constraints such as poor drainage and compaction, which limited vertical and lateral growth. Additionally, no pruning was performed at Spernal in 2023, as many trees were still too small. This likely contributed to the higher number of branches and pruning requirement observed in 2024, as uncorrected defects had accumulated over two seasons.

At the seed source level, L-P-C and Righi again stood out. These seed sources were among the tallest and had the most branches, yet they required relatively few corrective cuts. Their pruning ratios remained the lowest across both years, reinforcing the notion that high growth performance can coincide with desirable crown architecture. Escatalens and Sailershausen, by contrast, exhibited higher pruning ratios and a greater proportion of problematic branches, despite good overall growth. This suggests that while these seed sources are vigorous, their crown development may be more prone to structural defects.

The pruning type distribution provides further insight into qualitative differences in crown form. After the third growing season, most interventions involved removal of thick or ascending branches, and general balancing of crown architecture.

Sailershausen, Escatalens, and Tortoiseshell Wood had the highest frequencies of more severe pruning types, including removal of forks and double stems. By the fourth growing season, the proportion of severe pruning types had decreased at Fontmell and Sotterley. This shift reflects the corrective effect of earlier pruning interventions and suggests that crown structure improves with timely management.

To further explore the silvicultural impact of crown traits and pruning, a targeted correlation analysis was conducted. This revealed that trees with more branches and a higher number of pruned branches in 2023 tended to exhibit modestly greater height increment in 2024. The association was stronger for pruned branches than for total branch number, suggesting that formative pruning may effectively redirect growth into the main leader, particularly in trees with strong apical vigour. This supports the view that careful early pruning can enhance structural development without compromising growth.

However, these findings should be interpreted with care. The observed correlations were relatively weak and may not imply causality. It is equally plausible that more vigorous trees naturally produced more lateral shoots and responded better to pruning, rather than the pruning itself driving enhanced growth. Continued monitoring and future analyses will be essential to disentangle these effects and confirm whether the trend holds across later stages of stand development.

In summary, the best-performing seed sources — Righi, L-P-C, Escatalens, and Harcourt — combined wider branch angles, fewer ascending branches, and lower pruning requirements. This reduced early management demands while supporting the development of valuable, straight stems. Conversely, seed sources such as Ast Wood and Tortoiseshell Wood displayed less desirable crown traits, increasing the need for early intervention. These findings highlight the value of integrating both quantitative (e.g., branch number, pruning ratio) and qualitative (e.g., pruning type, branch angle) traits when evaluating performance. Selecting seed sources that maintain favourable crown architecture under varied site conditions — like L-P-C and Righi — may reduce silvicultural inputs and improve long-term timber value.

Phenological development and implications for adaptation

Phenology is a key adaptive trait in forest trees, influencing both survival and performance through its relationship with climate cues, frost risk, and growth potential. The spring and autumn phenological patterns observed in this trial revealed consistent variations between seed sources, reflecting their geographical origins and potential for local adaptation or maladaptation under current and future climatic conditions.

Spring phenology showed clear genetic differentiation. Righi flushed the earliest and was fully developed by early May, followed closely by Sailershausen, L-P-C, and Escatalens. These continental seed sources developed significantly earlier than the English, which flushed up to two weeks later. This aligns well with expectations based on latitude and elevation of origin. Earlier flushing is typically associated with continental provenances and warmer spring climates, while later flushing may be a frost avoidance strategy of northern or oceanic types.

Interestingly, Righi not only flushed earliest but also exhibited the highest apical shoot increment, highlighting the potential growth advantage of earlier development under low frost risk. However, this must be balanced against the higher vulnerability to late frosts—a factor not strongly expressed in this trial, but potentially relevant in colder springs. The consistently high growth and quality of Righi across multiple traits suggests that its phenological strategy is currently well-suited to southern English conditions.

Shoot growth patterns further support these interpretations. The continental seed sources generally exhibited stronger apical elongation than the English ones. While Stoopers Wood stood out as a positive exception—despite its delayed flush, it achieved one of the highest mean height increments—this appears to be due to a concentrated burst of growth later in the season, possibly a response to accumulated thermal time or competitive stress.

Autumn phenology extended this pattern. Righi, L-P-C, Sailershausen, and Rahay were among the last to enter dormancy, with green foliage still present in early December for some individuals.

In contrast, the English seed sources, and Harcourt showed earlier dormancy development, suggesting a shorter growing period. This longer season observed in the continental seed sources increases growth potential, but it also comes with increased risk if early autumn frosts occur—as was seen in mid-October, which likely triggered the sharp decline in dormancy stage across all seed sources. No evident frost damage was observed during the study, although it should be noted that no severe frost events occurred during the monitoring period.

The spring flush assessment in April 2024 confirmed these patterns at all sites, with continental seed sources again leading in development. This reinforces the reliability of the phenological observations at Spernal and suggests consistent phenological expression across sites.

Together, these findings indicate that the timing of leaf flush and dormancy in wild service tree is under strong genetic control but interacts with environmental factors such as photoperiod and temperature. The extended growing season of continental sources may offer a growth advantage under mild conditions but carries inherent risks in colder springs and autumns. Conversely, English seed sources may offer greater stability under harsher climates, though at the cost of lower growth potential.

In terms of selection and deployment, phenological traits should be considered alongside stem form and growth. Seed sources like Righi and L-P-C appear particularly promising, combining early flush, long growing season, strong apical dominance, and minimal dieback. However, their suitability under future frost regimes should be monitored, particularly in frost-prone or elevated sites.

4.1 Synthesis and implications for silviculture

The best-performing seed sources, Righi and L-P-C, combined vigorous height growth, favourable stem form, low forking, and efficient crown architecture with early flushing and a long growing season. These traits are highly desirable in high-quality timber production systems. Importantly, their performance was stable across sites, suggesting broad adaptability under current conditions in southern England.

Other continental seed sources such as Escatalens, Rahay, and Harcourt also performed well, especially in terms of stem quality and phenological timing. In contrast, the English seed sources, although expected to be well-adapted locally, showed slower growth and more frequent structural defects in the early years. Nonetheless, signs of catch-up growth and individual variation within these seed sources suggest potential for local improvement through selection.

Phenological observations revealed genetically stable timing of spring and autumn events, with continental seed sources flushing earlier and remaining active longer into the season. While this extended growing period enhances growth, it also increases exposure to frost damage — a trade-off that should be carefully considered in seed source deployment, particularly under future climate variability.

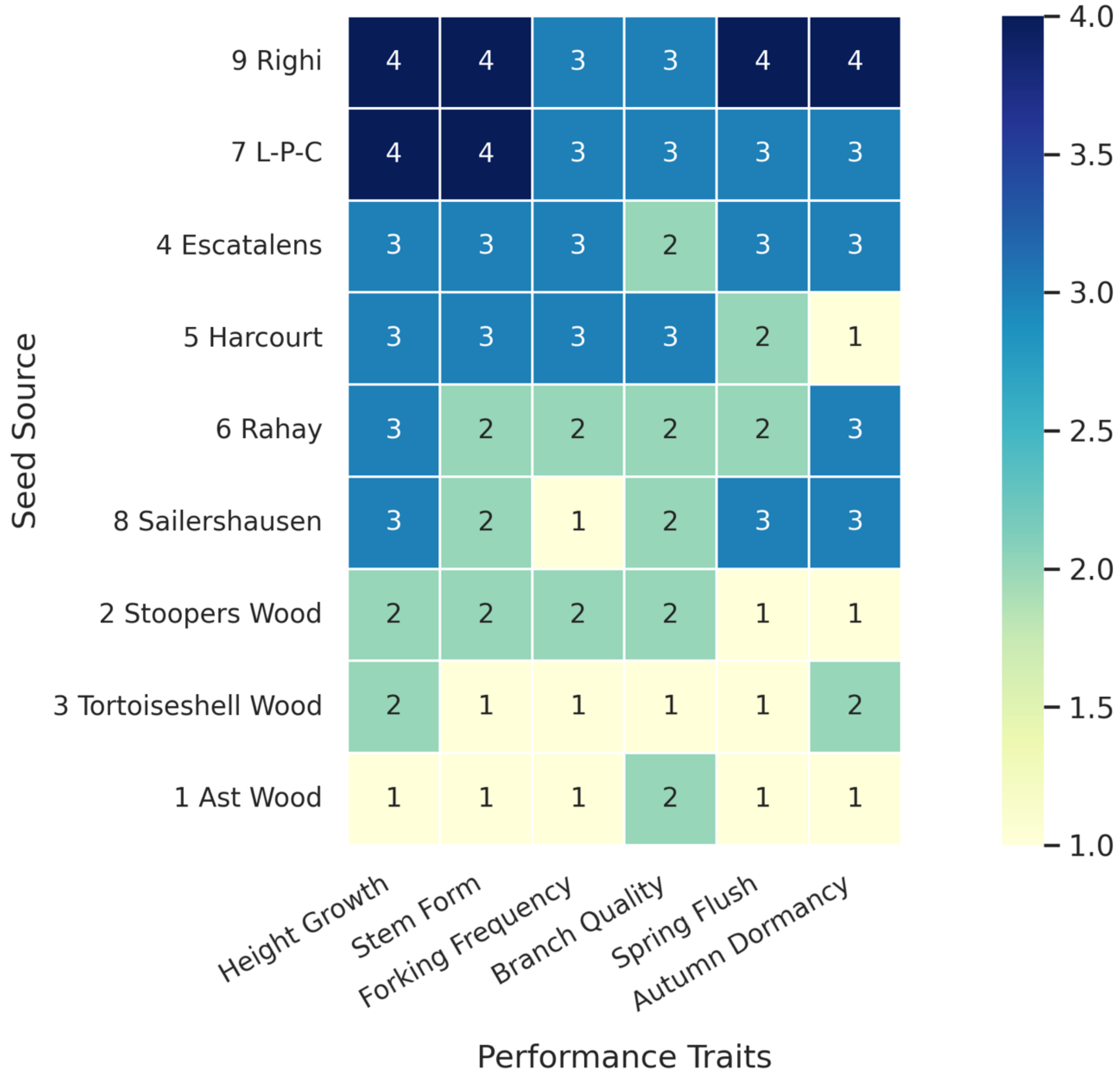

Figure 38. Summary of seed source performance.

Environmental conditions played a critical role. The Sotterley site, with its well-drained, warm soils and proactive site preparation, showed the highest growth and crown development, while Spernal, constrained by compacted soils, poor drainage, and competing ground vegetation, consistently underperformed. These findings reinforce the importance of early maintenance, site preparation, and moisture management, especially during establishment.

Genetic factors influenced early height growth and quality traits. Branching patterns and pruning requirements were found to be tightly linked to growth rate and crown architecture, with fewer but thicker branches in taller trees. This suggests that seed sources with strong apical dominance may reduce long-term silvicultural inputs.

Overall, the findings highlight the promising potential of selected continental seed sources for high-quality timber production under southern English conditions. Seed sources such as Righi and L-P-C exhibit the desirable combination of growth performance, timber form, and crown architecture that can support long-term silvicultural goals. However, their use should be accompanied by monitoring in frost-prone or marginal sites, and further research is needed on long-term performance, genetic structure, and adaptive capacity.

This trial lays the foundation for informed seed source selection in wild service tree and contributes to the broader effort of diversifying European forestry with alternative species suited to future climates. The early success of wild service trees in this trial suggests that — when matched to site and properly managed — this rare species may well have a strong future in mixed, climate-resilient forests.

4.1.1 Silvicultural recommendations and long-term implications

The results of this early-stage trial offer promising insights into the silvicultural potential of wild service tree under southern English conditions. While only four growing seasons have passed since establishment, several patterns are emerging that support practical recommendations for future planting, management, and potential integration into high-quality timber silviculture.

Selection of seed sources for timber production

Based on a composite evaluation of growth, stem form, apical dominance, crown architecture, and pruning requirements, the seed sources Righi, L-P-C, and to a slightly lesser degree Escatalens, Harcourt, and Rahay emerge as strong candidates for future timber-oriented planting. These seed sources consistently combined:

- Vigorous height growth and diameter increment
- Low frequency of structural defects such as forking and dieback
- Favourable branch architecture with wider branch angles and fewer severe pruning interventions

Notably, Righi and L-P-C achieved the best overall performance despite being sown late in the nursery, suggesting inherent genetic vigour and adaptability. Their ability to maintain straight form, combined with minimal apical damage or branching defects, supports their suitability for high-quality timber with limited corrective silvicultural input.

Site sensitivity, stand management, and silvicultural potential

Site conditions had a profound influence on growth and quality traits. Sotterley, with its well-drained subsoiled soil, mulching, and warmer microclimate, produced the tallest wild service trees with the most vigorous growth. In contrast, Spernal showed clear limitations in both growth and quality, likely due to waterlogging, compaction, and intense weed competition. Fontmell, while cooler and north-facing, offered consistent moisture and good soil aeration, contributing to high survival and uniform stand development.

These site-level outcomes emphasize the importance of:

- Careful site selection, avoiding poorly drained soils, compaction, and flat topography
- Mechanical site preparation and effective weed suppression
- Consistent management of competing vegetation in establishment phase
- Early irrigation, and water retention during extreme drought

Crown traits and branching structure also varied by seed source and were influenced by growth rate. A clear positive correlation was observed between tree height and branch number, suggesting that more vigorous individuals may require slightly more early maintenance. However, seed sources like Righi and L-P-C maintained favourable architecture with relatively low pruning demands, highlighting the value of integrated selection based on both vigour and form.

The results suggest that:

- Pruning needs vary substantially by seed source, and choosing high-performing types can reduce long-term management costs
- Early formative pruning (by years 3–4) is effective at correcting structural issues, particularly forks and ascending branches
- Monitoring phenological traits is important to mitigate frost risk, especially in continental seed sources

Overall, the performance of several continental seed sources — especially Righi and L-P-C — confirms the wild service tree's potential in high-quality hardwood systems in southern England and beyond. Its preference for mixed species stands, drought tolerance, as well as high economical- and ecological values makes it especially suitable for:

- Mixed species stands, especially alongside oak, maple, hornbeam, and possibly wild cherry
- Ecological forestry models aiming to increase biodiversity and climate resilience
- Noble hardwood production, targeting veneer or specialty sawn timber markets

Given its rarity in commercial forestry and valuable timber properties, the establishment of breeding populations and seed orchards should be prioritized for the best-performing seed sources. Furthermore, its favourable phenotypic plasticity and apparent early adaptability strengthen its candidacy for assisted migration to suitable sites in central and northern Europe under future climate scenarios.

Genetic considerations and broader relevance

The observed variations among seed sources are not only the result of site conditions and nursery treatment but are also strongly supported by underlying genetic variation. Previous studies have confirmed that wild service tree displays relatively high genetic diversity within and among populations across its range (Bednorz *et al.,* 2006; Demesure *et al.,* 2000; Oddou-Muratorio *et al.,* 2004; Angelone *et al.,* 2007). This genetic variability is crucial for its future adaptability under changing environmental conditions — particularly for rare species with fragmented distributions like wild service tree.

Notably, the Sailershausen seed source — included in both the current English trial and the long-term Liliental provenance trial in southern Germany — has previously demonstrated high growth and stem quality. In the Liliental provenance trial, the Sailershausen seed source demonstrated high early growth and stem quality, and it was also genetically analysed using nuclear microsatellites (Šeho *et al.,* 2018). The Sailershausen material showed a solid level of genetic diversity and some unique alleles, confirming its potential as a valuable source of genetic material for breeding and adaptation. However, it remains uncertain whether the Sailershausen batch used in this English trial derives from the exact same parent trees. This highlights the need for more precise provenance documentation and genetic fingerprinting in future trials to ensure comparability and traceability.

These findings are further supported by regional trials and genetic studies in Bavaria, where Sailershausen was identified as one of the best-performing provenances in terms of growth, stem form, and forking characteristics (Šeho *et al.,* 2021). Genetic analyses of 34 Bavarian wild service tree populations revealed distinct genetic clusters based on nuclear microsatellite markers (nSSRs), with Sailershausen belonging to one of the most promising groups. This provenance displayed high allelic richness and the presence of private alleles, indicating valuable genetic diversity.

Moreover, its strong performance under moderate temperatures (~8.5 °C) and relatively low annual precipitation (~700 mm) supports its relevance for climate-resilient forestry across central Europe and potentially in southern Scandinavia.

Given the scattered distribution and reliance on both clonal and sexual reproduction, conserving genetic variation will be essential in breeding and selection programs. To achieve this, future trials should incorporate genetic analyses using molecular markers (e.g., SSRs, SNPs) to map genetic structure, assess diversity within seed sources, and identify elite individuals. Such data will also be critical for certifying planting material and guiding provenance recommendations under future climate scenarios.

Risks and considerations of assisted migration

While the promising performance of certain continental seed sources — such as Righi and L-P-C — highlights their potential for deployment beyond their native range, including southern Scandinavia, assisted migration is not without risks. Translocating genetic material into new environments may lead to maladaptation if local conditions such as soil chemistry, photoperiod, or frost regimes differ substantially from the seed source's origin. Early flushing seed sources may be particularly vulnerable to late spring frosts in northern regions. There is also a risk of genetic swamping, where introduced seed sources hybridize with remnant local populations, potentially diluting locally adapted gene pools.

Furthermore, sourcing seed from a narrow genetic base — for example, a small number of mother trees — may reduce genetic diversity and future adaptive capacity. Ecological concerns include the potential for disruption of local communities, although the relatively non-competitive and non-invasive nature of wild service tree suggests low ecological risk in this regard.

Given these considerations, assisted migration of wild service tree should proceed cautiously, ideally through regional trials, genetic monitoring, and the use of a diverse range of seed sources. Such measures would support resilient forest establishment while mitigating unintended consequences of range expansion under climate change.

Applicability to southern Scandinavia and future outlook

Although this trial was established in southern England, many of the conditions—particularly the mild, moist winters and increasingly dry summers—mirror projected climate scenarios for southern Scandinavia (SMHI, 2024). The favourable performance of continental seed sources such as Righi and L-P-C under these conditions suggests that they may also thrive under similar environments in southern Scandinavia.

The potential for adaptation to northern climates is further supported by preliminary results from an international wild service tree experiment coordinated by Skovsgaard (2024). The trial was established in spring 2012 and includes 47 test sites distributed across England, Germany, Denmark, Norway, and Sweden — spanning a latitudinal gradient from approximately 50°N to just over 65°N *(Fig. 39)*. All trees in the experiment originate from the Sailershausen forest. Early results indicate a satisfactory survival rate across most sites and variable early growth, with particularly positive responses to weed suppression and higher soil fertility. The best early growth was observed in sites with moderate silt content and high base saturation, characteristics shared by fertile agricultural soils in southern Sweden.

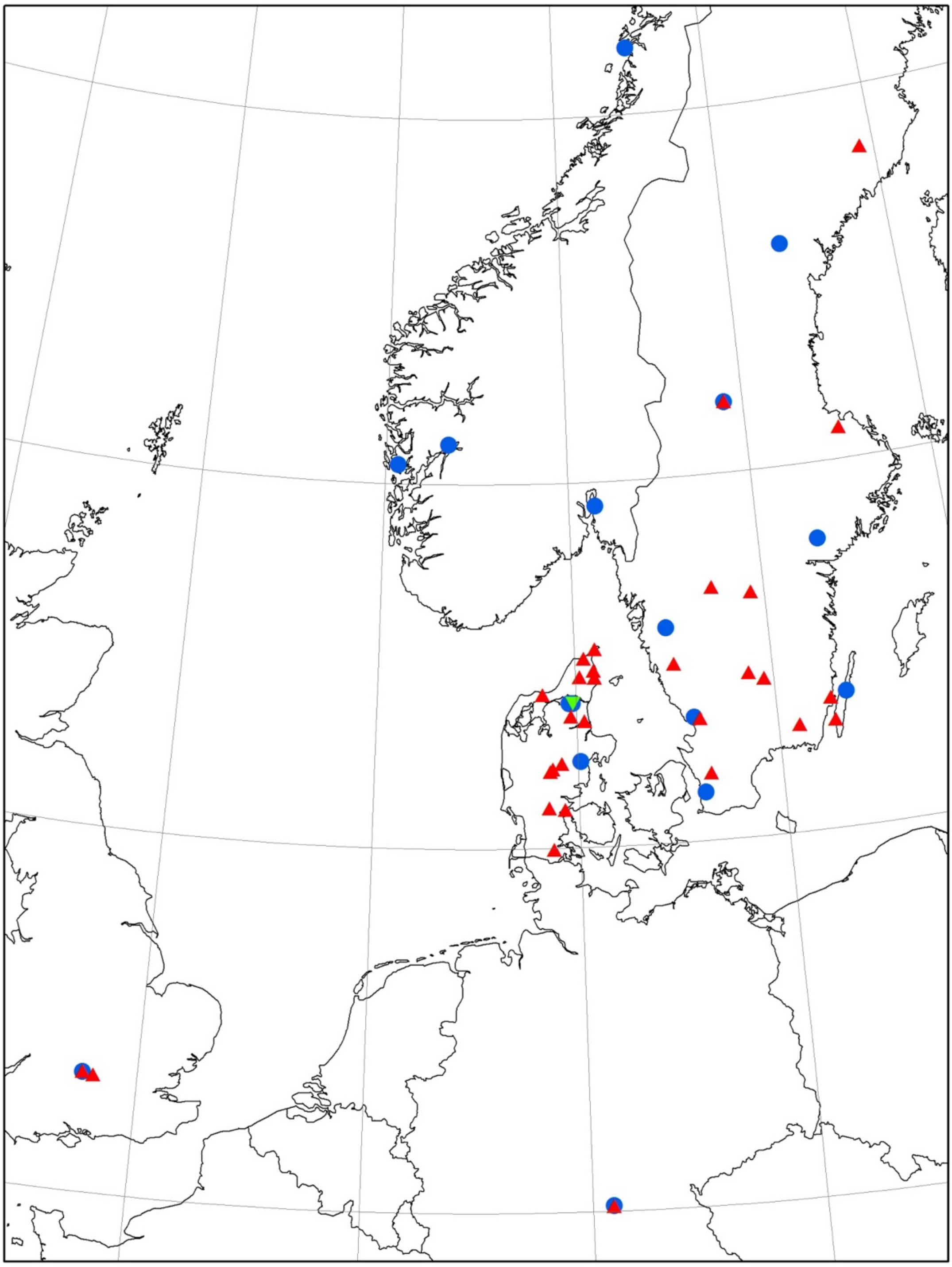

Figure 39. Location of the 47 experimental blocks in the international wild service tree experiment in Germany, Great Britain, Denmark, Sweden and Norway. The experiment was established spring 2012 with nursery stock of Sailershausen origin and range from 50° N (Sailershausen) to 66° N (Alstahaug). Legend: ● = agricultural land, ▲ = forest land, ▼ = chalk quarry. Each block includes four or six plots of contrasting establishment techniques (Skovsgaard, 2024).

4.1.2 Limitations and future research

While this study provides valuable early insights into the silvicultural potential of nine European seed sources of wild service tree, several limitations highlight the need for continued research. As the assessment is based on the first four growing seasons, it primarily reflects early establishment traits, and the long-term performance in terms of growth, structural quality, and climatic resilience remains unknown. Continued monitoring through mid-rotation and into maturity will be essential to evaluate how early leaders develop over time.

The study also treats each seed source as a genetic proxy, but the actual genetic diversity within seed sources is unknown. Future research should include molecular genetic analyses (e.g., SNPs, SSRs) to assess within-seed source variation, estimate heritability, and support selection of elite individuals for breeding.

Phenotyping methods based on visual scoring may introduce observer bias, particularly for traits like stem form and crown architecture; therefore, incorporating digital tools such as LiDAR, image analysis, or drone-based phenotyping would improve precision and reproducibility.

Phenological differences were observed among seed sources, but the absence of extreme weather events — such as late spring or early autumn frosts — limits conclusions about frost risk in early- or late-flushing genotypes. Continued phenological monitoring across more years and sites is necessary, particularly under growing climate variability. Furthermore, several site-level variables such as slope, microclimate, and vegetation competition were not directly measured, and installing environmental sensors (e.g., for soil moisture, temperature, and light) would enhance the resolution of future analyses.

The trial's geographic scope was limited to three sites in southern England, and broader testing across diverse environments — including Scandinavia, central Europe, and the Mediterranean — is needed to capture genotype × environment interactions and guide seed source deployment under future climates. These future efforts should also aim to identify and propagate elite trees from the existing population, supporting the establishment of seed orchards and targeted breeding for timber quality and adaptability.

4.2 Conclusion

This study presents the first seed source trial of wild service tree in England, offering valuable early insights into the survival, growth, stem quality, crown traits, and phenological development of nine European seed sources over the course of the first four growing seasons.

Clear variations were observed between seed sources and trial sites, highlighting the influence of both genetics and environment. The seed sources Righi and L-P-C, both of continental origin, consistently ranked among the top performers across multiple traits — including height growth, stem form, apical dominance, and crown architecture. Their favourable combination of rapid early growth and low pruning requirements suggests a strong genetic potential for high-value timber production under English conditions. The seed sources Escatalens, Harcourt, and Rahay demonstrated solid overall performance, with consistently good stem form and survival.

Site conditions played a decisive role in early establishment success. The best-performing wild service trees were found at Sotterley — a south-facing site with well-drained soils and thorough site preparation. Fontmell, while slightly behind in growth, exhibited the most uniform stand development and highest survival rates, likely due to a well-prepared site, aerated soils, and its north-facing aspect, which may have mitigated drought stress during the first and third growing seasons. In contrast, Spernal showed poor growth and lower survival, likely due to compacted soils, intense weed pressure, and impeded drainage. These findings underscore the critical importance of site selection, soil preparation, and early maintenance in the successful establishment of wild service tree plantations.

Crown traits — such as branch angle, density, and form — further emphasized differences between seed sources and underscored silvicultural implications. Notably, while faster-growing trees tended to produce more branches, the best-performing seed sources maintained favourable architecture with relatively low need for corrective pruning. A moderate correlation between height and branch number suggests that growth and quality traits can be balanced, particularly through careful seed source selection.

Phenological monitoring revealed consistent genetic variations in spring flush and autumn dormancy, with continental seed sources exhibiting longer growing seasons than their English counterparts. While this extended season likely contributes to their superior growth, it may also increase risk in frost-prone areas — a consideration for future deployment and site matching.

Taken together, these findings strongly support the potential of selected continental seed sources of wild service tree in afforestation programs targeting high-value hardwood production in England and climatically similar regions. With continued monitoring, integration of genetic data, and expansion of trials across climatic gradients, wild service tree could emerge as a valuable species for diversification, climate adaptation, and timber production in European forestry.

Figure 40. Righi tree in block 4 at Sotterley, April 25, 2024.

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Popular science summary

Tyskoxel *(Torminalis glaberrima)* är ett sällsynt lövträd med potential för framtidens klimatanpassade skogsbruk, tack vare sitt värdefulla virke, torktålighet och ekologiska egenskaper. I denna studie utvärderades nio olika frökällor från England, Frankrike, Tyskland och Italien i ett försök på tre platser i södra England, under de första fyra växtsäsongerna efter plantering. Tyskoxeln planterades i blandbestånd tillsammans med ek *(Quercus robur),* naverlönn *(Acer campestre)* och avenbok *(Carpinus betulus).* Syftet var att identifiera vilka frökällor som lämpar sig bäst för högkvalitativ virkesproduktion i blandade lövskogssystem under tempererade förhållanden.

Två kontinentala frökällor – Righi (Italien) och Lugny-Plottes-Chardonnay (Frankrike) – utmärkte sig genom snabb tillväxt, rak stamform och ett grenverk som krävde minimal beskärning. Tre frökällor, Escatalens, Harcourt och Rahay (från franska fröplantager), visade också goda resultat men med något lägre tillväxt. Sailershausen (Tyskland) visade god tillväxt och bra stamform, men hade dock en högre förekomst av klykor. De engelska frökällorna hade generellt långsammare tillväxt och sämre stamform under de första åren, men vissa individer visade potential för framtida trädförädlingsprogram.

Skillnaderna mellan försökslokalerna var tydliga. Den bästa tillväxten noterades på Sotterley, en varm och väldränerad sydsluttning med god markberedning och aktiv tidig skötsel. Fontmell hade den jämnaste beståndsutvecklingen och högst överlevnad, medan Spernal hade sämst resultat på grund av kompakterad jord, dålig dränering och hög konkurrens av markvegetation.

De kontinentala provenienserna hade både tidigare lövsprickning och invintrade senare, vilket gav längre växtsäsong och hög tillväxt – men också en ökad risk för frostskador. I det här försöket förekom dock inga allvarliga frostskador

Studien visar att tyskoxel kan ha en plats i framtidens lövskogsskötsel, särskilt i blandbestånd och torrare miljöer. Valet av rätt frökälla och lokal är avgörande för att lyckas. Fortsatt forskning och långsiktig uppföljning krävs för att säkra de bästa genetiska resurserna och skapa framtidens robusta lövskogar.

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Appendix 1

Fontmell Hill Estate – Soil Analysis by Christopher Guest. Lab results by Yara UK Ltd. Date of survey: 19-Nov-19. Last Updated 31-Jan-20

Block	Depth of Profile (cm)	Groundwater Present	Reduction/ Mottling	Plough Layer Depth	HCL Reaction (A Horizon)	HCL Reaction (B Horizon)	HCL Reaction (C Horizon)	Horizons Present	Soil Texture Classification	Soil Type
FME-01	100	No	No	32cm	Yes	Yes	Yes	B (37cm), C+	Clay Loam	Calcareous Brown Earth
FME-02	100	No	No	32cm	Yes	Yes	Yes	B (44cm), C+	Clay Loam	Calcareous Brown Earth
FME-03	100	No	No	28cm	Yes	Yes	Yes	B (30cm), C+	Sandy Clay Loam	Calcareous Brown Earth
FME-04	60	No	No	30cm	Yes	Yes	Yes	B (18cm), C+	Sandy Clay Loam	Calcareous Brown Earth

	pH	P	K	Mg	Ca	Cu	S	Mn	Na	Zn	B
		ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm
FME-01	8,0	9	101	47	3466	2	5	32	16	4	1
FME-02	7,9	11	90	42	3418	2	5	30	17	4	1
FME-03	8,2	6	82	35	3134	2	4	30	16	2	1
FME-04	7,9	10	120	41	3586	3	3	29	18	3	1
Average	**8**	**9**	**98**	**41**	**3401**	**2**	**4**	**30**	**17**	**3**	**1**

	Organic Carbon (%)	Total Nitrogen (%)	CEC	Organic Matter	C:N Ratio	Sand (%)	Silt (%)	Clay (%)
			(meq/100g)	DUMAS (%)				
FME-01	1,7	0,16	14,8	2,9	10,5	43	37	21
FME-02	1,8	0,15	14,5	3,1	12	40	39	21
FME-03	0,9	0,08	13,2	1,6	11,6	54	20	26
FME-04	1,4	0,14	15,3	2,4	10	66	16	19
Average	**1,5**	**0,13**	**14**	**3**	**11**	**51**	**28**	**22**

Sotterley Estate – Soil Analysis by Christopher Guest. Lab results by Yara UK Ltd. Date of survey: 21-Nov-19. Last Updated 31-Jan-20

Block	Depth of Profile (cm)	Groundwater Present	Evidence: Reduction/Mottling	Plough Layer Depth	HCL Reaction (A Horizon)	HCL Reaction (B Horizon)	HCL Reaction (C Horizon)	Horizons Present	Soil Texture Classification	Soil Type
SOE-01	110	No	B & C Horizons	30cm	No	Yes (mild reaction- specks chalk present)	Yes	B (35cm), C+	Clay	Surface water Gley
SOE-02	100	Yes (at 97cm)	B & C Horizons	35cm	No	No	Yes	B (33cm), C+	Clay	Surface water Gley
SOE-03	100	Yes (at 110cm)	B & C Horizons	33cm	No	Yes (mild reaction- specks chalk present)	Yes	B (28cm), C+	Clay Loam	Surface water Gley
SOE-04	100	Yes (at 96cm)	B & C Horizons	36cm	No	No	Yes	B (27cm), C+	Sandy Clay	Surface water Gley

	pH	P	K	Mg	Ca	Cu	S	Mn	Na	Zn	B
		ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm
SOE-01	8,0	4	126	86	4053	3	2	29	40	2	1
SOE-02	7,8	3	104	85	3528	3	1	28	39	1	1
SOE-03	7,9	3	112	86	4179	3	3	30	39	1	1
SOE-04	7,7	3	113	71	3765	3	1	44	28	1	1
Average	**7,9**	**3**	**114**	**82**	**3881**	**3**	**2**	**33**			

	Organic Carbon (%)	Total Nitrogen (%)	CEC (meq/100g)	Organic Matter DUMAS (%)	C:N Ratio	Sand	Silt	Clay
SOE-01	0,70	0,070	17,8	1,2	10	35	30	35
SOE-02	0,50	0,040	15,4	0,8	11,6	41	23	36
SOE-03	0,80	0,060	18,3	1,3	12,6	35	36	28
SOE-04	0,8	0,07	16,3	1,4	11,6	48	19	32
Average	**0,70**	**0,06**	**17**	**1**	**11**	**40**	**27**	**33**

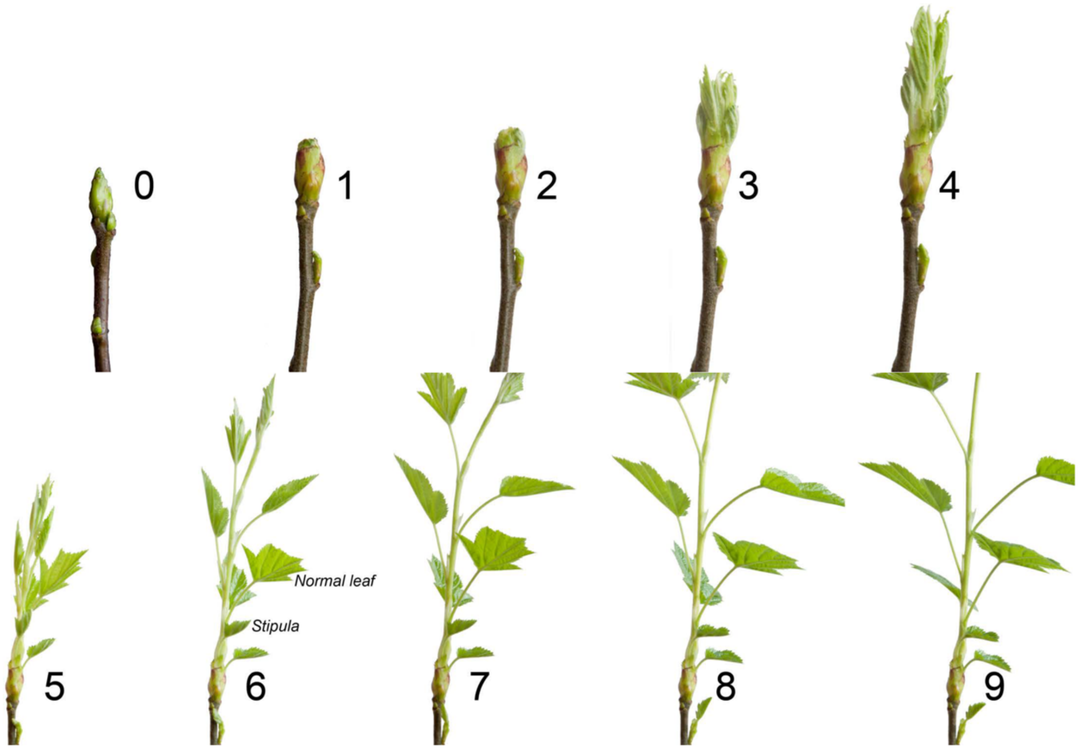
Spernal Estate – Soil Analysis by Christopher Guest. Lab results by Yara UK Ltd. Date of survey: 30-Jan-20. Last Updated 31-Jan-20

Block	**Depth of Profile (cm)**	**Groundwater Present**	**Evidence: Reduction/Mottling**	**Plough Layer Depth**	**HCL Reaction (A Horizon)**	**HCL Reaction (B Horizon)**	**HCL Reaction (C Horizon)**	**Horizons Present**	**Soil Texture Classification**	**Soil Type**
SPE-01	95	No	B & C Horizons	30cm	No	No	Yes	B (26cm), C+	Silty Clay Loam	Surface water gley
SPE-02	100	Yes (at 98cm)	B & C Horizons	26cm	No	No	Yes	B (37cm), C+	Clay Loam	Surface water Gley
SPE-03	100	No	B & C Horizons	30cm	No	No	Yes	B (28cm), C+	Clay Loam	Surface water Gley
SPE-04	100	No	B & C Horizons	28cm	No	Yes	Yes	B (28cm), C+	Clay Loam	Surface water Gley

	pH	**P**	**K**	**Mg**	**Ca**	**Cu**	**S**	**Mn**	**Na**	**Zn**	**B**
		ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm
SPE-01	7,9	7	312	219	6390	12	5	52	31	5	6
SPE-02	8,2	2	208	377	5341	6	9	39	44	1	4
SPE-03	8,3	3	271	436	5309	5	18	55	45	2	3
SPE-04	8,3	2	211	228	5294	4	9	47	31	1	2
Average	8,2	**3,50**	**251**	**315**	**5584**	**7**	**10**	**48**			

	Organic Carbon (%)	**Total Nitrogen (%)**	**CEC (meq/100g)**	**Organic Matter DUMAS (%)**	**C:N Ratio**	**Sand**	**Silt**	**Clay**
SPE-01	2,7	0,28	29,5	4,6	9,6	14	57	29
SPE-02	1	0,08	25,8	1,7	12,4	38	31	31
SPE-03	1,1	0,08	26,2	1,9	13,8	39	31	30
SPE-04	0,9	0,06	24,4	1,5	14,5	42	25	33
Average	**1,43**	**0,13**	**26**	**2**	**13**	**33**	**36**	**31**

Appendix 2



Phenological stages for wild service tree. 0: dormant, 1: bud burst and leaf emergence, i.e. bud stretching and bud scales separate, 2: shoot and leaves protrude from tip of bud, 3: leafing, i.e. first leaf visible, but folded; petiole not visible, 5: first leaf completely unfolded, but lamina wrinkled; petiole visible, 7: first leaf completely unfolded and lamina flattened, 9: all leaves completely unfolded and all lamina flattened. (Skovsgaard, 2015).

Appendix 3

Autumn phenology stages for wild service tree

Stage	Description	Leaf Condition	Notes
9	Fully green	100% green leaves, new apical shoot flushing	Active shoot growth
8	Start of leaf coloration	90–95% green leaves	Apical shoot still growing
7	Early stage of leaf coloration	80–90% green leaves	Buds hardening
6	Late early stage of leaf coloration	65–75% green leaves	Buds hardened
5	Halfway through leaf coloration	50–60% green leaves	—
4	Just beyond halfway through coloration	40–50% green leaves	Beginning to shed leaves
3	Late stage of coloration	<50% green leaves	More than half of leaves shed
2	End of coloration, active shedding	20–30% of leaves remain	—
1	Final stage of coloration	0–10% of leaves remain	—
0	Complete leaf fall	All leaves shed	Full dormancy onset

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