INDOOR SEED PRODUCTION OF SILVER BIRCH (*BETULA PENDULA* ROTH): CURRENT KNOWLEDGE AND RESEARCH NEEDS

***Aldis Sproģis[1], Alise Bleive[2], Kaspars Liepiņš[1,2]**
[1]Latvia University of Life Sciences and Technologies, Jelgava
[2]Latvian State Forest Research Institute Silava, Latvia
*Corresponding author's email: aldis.sprogis@silava.lv

Abstract
Silver birch is the most economically important deciduous tree species in the Nordic and Baltic countries and represents a key raw material for the rapidly expanding plywood and wood-based panel industries. Although birch, as a pioneer species, primarily regenerates naturally, the use of genetically improved reproductive material can substantially increase stand productivity and improve stem quality. Reliable production of genetically superior seed is therefore a critical prerequisite for sustainable birch forestry. A technology for intensive birch seed production in plastic-covered seed orchards, originally developed in Finland, has been adopted across Northern Europe, enabling seed production within only a few years after orchard establishment. However, operational experience in Latvia and other countries indicates large variation in seed yield, regularity, and quality between years and orchards. These inconsistencies are largely driven by poorly understood interactions between orchard microclimate, genetic background (clone composition), and reproductive phenology, as well as by limitations in pollination processes under controlled environments. This narrative review synthesizes current knowledge on birch seed production in plastic-covered orchards with a specific focus on Nordic and Baltic conditions. We summarize existing management practices, experimental findings, and ongoing research efforts, and identify critical knowledge gaps related to flowering induction, pollination efficiency, microclimate regulation, and clonal selection. The review defines priority research directions required to achieve earlier, more regular, and higher seed yields, and provides a scientific basis for improving seed supply systems supporting large-scale forest regeneration under changing climatic conditions.
Keywords: reproductive phenology, forest tree breeding, seed orchards, seed yield stability, flowering induction.

Introduction

Forests provide a wide array of ecosystem services that are essential for human well-being and sustainable economic development, including the provisioning of timber as a key resource for the bioeconomy and long-lived wood products. In Europe, boreal and temperate forests not only contribute to climate regulation, water purification, and biodiversity conservation, but also underpin regional industrial sectors such as wood-based panel and plywood manufacturing (European Environment Agency, 2023, 2024; Eurostat, 2026). The strategic importance of forest ecosystems is reflected in national and international policies recognising forests as multifunctional landscapes that supply both ecological and socio-economic benefits (Ministry of Agriculture of the Republic of Latvia, 2018).

Improving forest productivity and adaptive capacity under changing climatic conditions has become a central objective of forestry research and practice. Historically, tree breeding and genetic improvement efforts have focused on enhancing growth, wood quality and vitality, particularly in conifer species such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) in the Northern European context (Danell, 1991; Egbäck et al., 2018). However, there has been an increasing emphasis on broadening breeding goals to include genetic diversity and resilience to environmental change, reflecting the need to support ecosystem health and long-term sustainability under global change pressures (Li et al., 2025).

Within this broader framework, deciduous tree species have received growing attention in breeding and forest management programmes (Gailis, 2026; Liziniewicz et al., 2022; Rosvald, 2011). Among these, silver birch (*Betula* pendula Roth) and downy birch (*Betula pubescens* Ehrh.) are ecologically and economically significant across the Baltic Sea region (Hynynen et al., 2009). Birches occur widely in boreal and temperate forests, contribute to biodiversity and soil functioning, and play a role in early successional dynamics, while their wood is highly desired in plywood production and bio-based material value chains (Cakiroglu et al., 2019; Dubois et al., 2020; Jonczak et al., 2020).

The heightened demand for high-quality birch timber, driven by both domestic industry and bio-refining innovation, has stimulated interest in advancing reproductive and silvicultural systems that can deliver improved seed supply. Additionally, ensuring sustainable domestic supply chains is of strategic importance in many countries, as disruptions caused by global geopolitical and trade uncertainties underscore the vulnerability of imported reproductive material and wood resources.

Compared with conifer species, breeding cycles in birch can be completed substantially faster due to its earlier onset of flowering and shorter generation intervals, allowing more rapid genetic gain (Hynynen et al., 2009; Koski & Rousi, 2005). In addition, the establishment of seed orchards in indoor facilities, such as plastic-covered greenhouses, enables intensive management and has been shown to result in abundant seed yields already a few years after orchard establishment (Ahtikoski, 2000; Lepisto, 1973).

Plastic-covered greenhouse seed orchards enable high genetic control and regulated seed production through pollen isolation and controlled environments, their high costs, technical complexity, limited integration with field forestry, and potential risks related to seed quantity, viability and clonal balance represent important constraints (Wilson, 2015).

Indoor birch seed orchards were first developed in

Finland in early seventies of last century, where this technology was introduced to accelerate seed production and improve genetic control, and it has since been adopted in several countries like Sweden, Baltic countries, Iceland, Germany and China (Poykko, 2007). Although general management principles for birch seed orchards have been described by Finnish specialists (Poykko, 2013), the physiological thresholds and reproductive conditions underpinning regular and abundant seed production remain insufficiently defined.

Despite decades long use of plastic-covered greenhouse seed orchards and the availability of general management guidelines, practical experience demonstrates that seed production in birch orchards often remains irregular (Isio, 2024). Substantial inter-annual variation is frequently observed not only in seed yield but also in seed quality parameters, such as viability and germination capacity. These fluctuations indicate that the biological regulation of flowering, pollination success and seed development under controlled greenhouse conditions is still incompletely understood. In particular, the relative roles of internal physiological factors and external environmental conditions in driving year-to-year variation in reproductive output have received limited empirical attention.

This knowledge gap constrains the optimisation of intensive birch seed production systems and limits the predictability and reliability of genetically improved seed supply, which is increasingly critical for both breeding programmes and forest regeneration strategies.

The aim of this review is to synthesise existing knowledge on birch seed production in plastic-covered greenhouse seed orchards and to identify key research gaps limiting the predictability, regularity and quality of seed yields. By evaluation of current management approaches, biological processes and environmental controls described in the literature, this review seeks to define priority directions for future research needed to optimise intensive birch seed production systems and support reliable supply of genetically improved reproductive material for forest regeneration.

Materials and Methods

Literature search

This review is based on a comprehensive survey of peer-reviewed scientific literature focusing on Silver birch (*Betula pendula* Roth) flowering, seed production and the management of plastic-covered greenhouse seed orchards. Literature searches were conducted primarily using the bibliographic databases Scopus and Web of Science, which were selected due to their broad coverage of forestry, plant physiology and applied silviculture research. Additional sources were identified through reference list screening of key publications and relevant monographs, conference materials and institutional reports where appropriate.

Search queries combined terms related to species, reproductive biology and seed production systems. The core search strings included, but were not limited to: ‘birch flowering’, ‘flower induction’, ‘reproductive phenology’, ‘seed orchard management’, ‘plastic-covered greenhouse’, ‘controlled environment seed production’, and ‘*Betula* seed yield’.

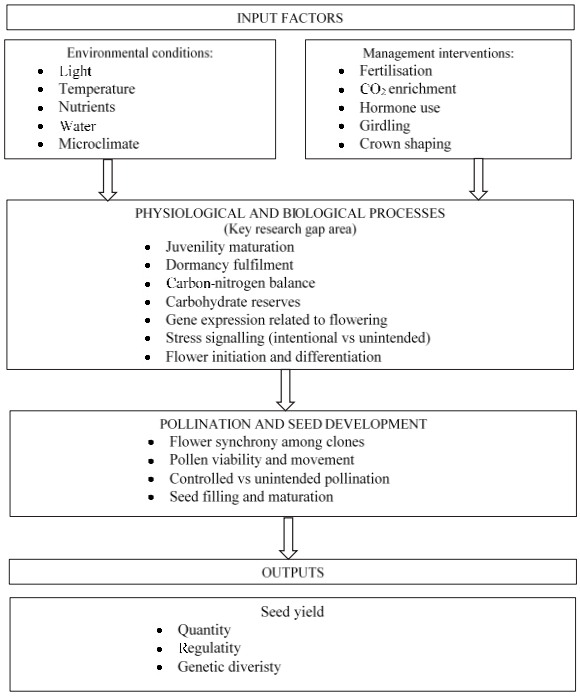
Search terms were applied in various combinations and adjusted iteratively to ensure comprehensive coverage of the topic.

Scope and synthesis approach

The review follows a structured narrative approach, integrating findings from experimental studies, applied seed orchard research and physiological investigations. Particular emphasis was placed on identifying consistencies and discrepancies among studies, as well as areas where empirical evidence remains limited or fragmented. In total, 58 literature sources were systematically reviewed and synthesised in this study.

Figure 1

Interactions among environmental conditions, management interventions and genetic factors influencing flowering initiation and seed crop in plastic-covered birch seed orchards



Conceptual framework

To support synthesis and interpretation, this review proposes the development of a conceptual framework illustrating the principal biological, environmental and management-related factors influencing seed yield and quality in plastic-covered birch seed orchards. Such a schematic representation is intended to clarify interactions among flowering induction, pollination processes, clonal effects and controlled environmental conditions, and to assist in identifying priority directions for future research.

Figure 1 synthesises the key environmental, management

and genetic factors influencing reproductive processes in plastic-covered birch seed orchards. Environmental conditions (light, temperature, nutrients and water regime) interact with silvicultural interventions such as fertilisation, CO_2 enrichment, crown management and controlled stress treatments, while clonal genetic characteristics determine inherent flowering capacity and phenological patterns.

These inputs act through underlying physiological processes, including maturation status, dormancy fulfilment, carbohydrate dynamics and gene activity related to flowering induction, which ultimately regulate pollination success, seed development and reproductive allocation. The resulting outputs are expressed as seed yield, yield stability and seed quality. Regulatory requirements concerning genetic diversity and reproductive material zoning operate across all levels of the system. The framework highlights the central role of physiological mechanisms as a key area where further research is needed to improve the predictability and efficiency of intensive birch seed production systems.

Results and Discussion

Reproductive cycle of silver birch

Silver birch is a monoecious, wind-pollinated tree species whose reproductive ecology is well documented. The initiation of reproductive primordia takes place during the preceding growing season, typically in mid- to late summer, when male and female inflorescences are differentiated within axillary buds on current-year shoots. Male catkins develop earlier and overwinter as externally visible structures, whereas female inflorescences remain enclosed within buds (Sarvas, 1952; Vakkari, 2009). Following winter dormancy, flowering occurs in early spring, often shortly before or concurrently with leaf flushing, with pollen release from male catkins and subsequent wind-mediated pollination of receptive female flowers (Atkinson, 1992; Hynynen et al., 2010).

Successful pollination, fertilisation and seed development depend on synchrony between pollen shedding and female receptivity, favourable spring weather conditions and adequate physiological status of the trees. Seed development proceeds throughout the summer, with maturation and dispersal occurring in late summer to early autumn. This reproductive strategy results in pronounced inter-annual variability in seed yield, as reproductive success is influenced by environmental conditions during both the year of floral initiation and the subsequent flowering and seed development phases (Hynynen et al., 2010; Pelham et al., 1984; Sarvas, 1956). Birch typically produces some seed annually, while abundant seed crops often occur at intervals of approximately two to three years (Cameron, 1996; Holm, 1994).

Genetic diversity and reproductive synchrony in seed orchards

The conservation of genetic diversity is a key consideration in the design and management of forest tree breeding and seed production systems (Ivetić et al., 2016). In seed orchards established for the production of forest reproductive material, it is essential to ensure adequate representation of selected genotypes and effective cross-pollination among them. Consequently, seed orchards typically include multiple superior clones selected for desirable traits such as growth performance, vitality and stem quality. For these orchards to function as intended breeding populations, however, it is crucial that the participating clones contribute to gene exchange through successful flowering and pollination (Eriksson et al., 2013; Lindgren & Prescher, 2005).

Even when several dozen clones are represented within a seed orchard, effective cross-pollination may remain limited if flowering intensity is low or uneven among clones. Differences in reproductive characteristics including the age at first flowering, flowering intensity and the temporal pattern of reproductive development are known to have a strong genetic component in many forest tree species (Kang, 2003; Owens & Blake, 1985). In addition, the phenology of flowering may vary substantially among clones. In wind-pollinated species such as birch, the flowering period of individual trees may be very short, sometimes lasting only a few days, meaning that asynchronous flowering among clones can significantly reduce opportunities for cross-fertilization and lead to unequal parental contributions to the seed crop (Sarvas, 1952).

Plastic-covered seed orchards offer important advantages for controlling pollination processes. The physical barrier created by the plastic covering can effectively reduce contamination from external pollen sources, while the warmer microclimate often accelerates reproductive development and leads to earlier flowering compared with natural stands. These conditions may substantially increase the genetic value of the produced seed by ensuring that pollination occurs primarily among the selected orchard clones (Harju & Nikkanen, 1996; Ruotsalainen, 2014). However, such controlled systems also place greater responsibility on orchard design and management to maintain adequate genetic diversity and balanced parental contributions over time.

For this reason, the selection of clones for seed orchard establishment should consider not only breeding traits such as productivity and quality but also reproductive characteristics, including flowering capacity and phenological compatibility.

Juvenile phase and reproductive maturity in birch

One of the key biological advantages of birch in forest reproductive material production is its relatively short juvenile phase compared with many economically important conifer species. In natural stands, silver birch typically begins producing flowers and viable seeds at approximately 10–15 years of age (Perala & Alm, 1990). This contrasts with species such as Norway spruce and Scots pine, where the onset of regular seed production often occurs several decades after stand establishment. The relatively early onset of

seed production in birch therefore represents an important advantage for breeding programmes and seed orchard establishment, enabling shorter breeding cycles and earlier availability of genetically improved reproductive material.

The transition from the juvenile vegetative phase to the generative phase represents a critical developmental threshold in woody plants. During the juvenile stage, trees are physiologically incapable of forming reproductive structures regardless of environmental conditions (Zimmerman, 1972). Only after this phase has been completed do trees acquire reproductive competence and become capable of initiating floral buds (Hackett & Murray, 1993).

Shortening the juvenile phase through the induction of early flowering has been identified as an important objective in the breeding of woody perennials (Khan et al., 2025). Experimental studies indicate that flowering in birch can occur at a very early developmental stage: under controlled conditions, reproductive structures have been observed in individuals as young as 8–30 months after germination (Longman, 1976; Longman & Wareing, 1959).These observations suggest that reproductive competence may develop early in the ontogeny of birch, although under natural conditions flowering usually occurs later, once sufficient crown development and resource accumulation have been achieved.

Understanding the factors that regulate the transition from vegetative growth to reproductive development is therefore essential for improving the efficiency of birch seed production systems.

Environmental and physiological triggers of flowering

The transition from vegetative growth to reproductive development in woody plants is controlled by a complex interplay of environmental cues and internal physiological signals (Khan et al., 2025; Wang et al., 2024). In temperate tree species, floral initiation is typically regulated by seasonal changes in environmental conditions, including photoperiod, temperature and resource availability, which interact with endogenous developmental processes to determine the timing and intensity of flowering (Wilkie et al., 2008). In birch, reproductive buds are generally initiated during the previous growing season (Dahl & Strandhede, 1996), indicating that environmental conditions experienced during summer may play a crucial role in determining the following year's flowering intensity and seed crop.

Light availability and temperature are among the most important environmental factors influencing flowering in trees. Long photoperiods and favourable temperature conditions during the growing season can promote the formation of reproductive buds (Almqvist, 2018; Tooke & Battey, 2010).

Carbon availability and the carbon–nitrogen (C:N) balance are widely considered important physiological factors influencing the initiation of flowering in woody plants. Classical plant physiology concepts suggest that relatively high carbon availability, or a higher C:N ratio, tends to favour reproductive development, whereas high nitrogen availability typically promotes vegetative growth. Early studies on woody plant development noted that the accumulation of carbohydrates in shoots and buds often coincides with periods of floral bud initiation (Kozlowski & Pallardy, 1997; Zimmerman, 1972). In forest trees, stored carbohydrates provide both energy and structural carbon for the formation of reproductive organs, and several studies indicate that greater carbon reserves may contribute to increased flowering intensity in subsequent seasons (Hoch, 2005).

Hormonal and genetic regulation of floral initiation

The transition to flowering in woody plants is regulated by complex genetic networks integrating environmental signals and internal physiological status. Among the genes associated with floral induction in birch, particular attention has been given to the MADS-box transcription factor BpMADS4, which is homologous to floral identity genes involved in the regulation of reproductive development in many angiosperms. Experimental overexpression of BpMADS4 in silver birch has been shown to induce precocious flowering, with transgenic trees producing inflorescences within the first year of growth (Elo et al., 2007; Lemmetyinen et al., 2004).

In addition to genetic regulation, plant hormones are widely known to influence floral initiation in woody perennials. Applications of gibberellins, cytokinins, or other growth regulators have been successfully used to stimulate flowering in several forest tree species, particularly conifers such as *Picea* and *Pinus* in seed orchard management (Owens & Blake, 1985; Pharis & King, 1985). However, comparable experimental evidence for effective hormone-induced flowering in birch is limited.

Stress-induced flowering responses

Stress-related physiological responses are known to influence the transition from vegetative to reproductive development in many woody plants. Numerous studies demonstrate that abiotic and biotic stressors can modulate hormonal signalling networks regulating floral induction, including changes in gibberellins, cytokinins, auxins and abscisic acid, which affect meristem identity and the initiation of floral buds (Li et al., 2024; Sun et al., 2022). Moderate stress often reduces vegetative vigour, thereby altering internal resource allocation in ways that favour reproductive development. Such conditions are frequently associated with increased carbohydrate accumulation in buds and shoots, shifts in the carbon–nitrogen balance, and changes in assimilate partitioning, all of which are recognised as important physiological cues for floral initiation in woody perennials (Song et al., 2024; Sun et al., 2022).

Stress-inducing silvicultural practices that simulate drought or disrupt vascular transport such as stem or branch girdling are widely used to manipulate reproductive development in conifer seed orchards

(Wheeler et al., 1985). Experimental studies on silver birch have shown that partial root excision and soil-drying treatments significantly alter stomatal conductance, root-to-shoot signalling and carbon allocation patterns, creating physiological conditions associated with moderate stress (Fort et al., 1998). Although these studies primarily examined physiological responses to water stress, they suggest that stress-induced changes in resource allocation and hormonal signalling may potentially influence reproductive activity in birch grown under controlled seed orchard conditions.

Future research directions for improving flowering and seed production in birch seed orchards

Despite considerable knowledge about the reproductive biology of silver birch, several important aspects of flowering regulation and seed production remain insufficiently understood. Context of intensive existing studies provide valuable insights into the ecological, physiological and molecular mechanisms underlying flowering in woody plants, however, the integration of these processes into practical seed production systems remains limited. This is especially relevant for plastic-covered seed orchards, where environmental conditions, pollination dynamics and tree physiology differ substantially from those in natural stands.

Identifying the physiological thresholds that trigger reproductive bud formation in birch is a critical research need. Although environmental cues such as photoperiod, temperature and resource availability are known to influence flowering, the specific combinations of factors required to consistently initiate floral development remain poorly defined. In particular, further research is needed to clarify the role of carbohydrate reserves, carbon–nitrogen balance and tree nutritional status in regulating flowering intensity under orchard conditions.

Another important research direction relates to the synchronisation of flowering among clones in seed orchards. Genetic variation in flowering phenology and reproductive capacity can lead to unequal parental contributions to the seed crop, potentially reducing the effective population size and genetic diversity of the produced reproductive material. Future studies should therefore investigate the extent of clonal variation in flowering timing and intensity in birch seed orchards.

Further research is also needed to evaluate the effectiveness of stress-based management practices for stimulating flowering in birch. While techniques such as drought stress, root pruning or girdling have been widely used to enhance reproductive activity in conifer seed orchards, comparable experimental studies in birch remain scarce. Investigating how controlled stress treatments influence hormonal signalling, resource allocation and floral induction in birch could provide valuable tools for improving reproductive performance in intensive seed production systems.

Overall, advancing knowledge in these areas will be essential for developing more reliable and efficient birch seed production systems capable of supporting forest regeneration and tree breeding programmes under changing environmental and socio-economic conditions.

Conclusions

1. Silver birch possesses several biological characteristics that make it particularly suitable for intensive seed production systems, including early reproductive maturity and relatively short breeding cycles compared with many economically important conifer species. The initiation of flowering in birch is controlled by a complex interaction of developmental stage, environmental conditions and internal physiological processes, including carbon balance, hormonal regulation and genetic control mechanisms.
2. Plastic-covered seed orchards provide important opportunities to improve the genetic quality and reliability of birch seed production by enabling control of pollination and orchard microclimate. However, several key knowledge gaps remain. In particular, further research is required to determine the physiological thresholds that trigger floral initiation in birch, to understand the genetic and phenological variation in flowering among clones and its impact on reproductive synchrony, and to evaluate the potential of stress-based management practices to stimulate flowering under controlled orchard conditions.
3. Addressing these research gaps will be essential for developing management strategies that ensure both regular seed production and balanced genetic contributions among clones, thereby maintaining the genetic diversity and long-term sustainability of birch seed orchard systems.

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