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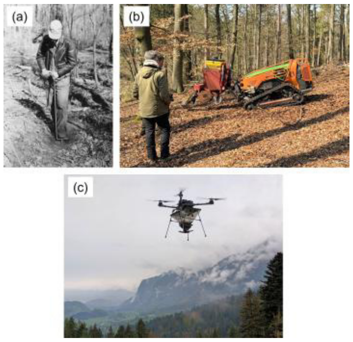

International practices for regenerating and restoring forest trees by seeding – an introduction

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Abstract

This manuscript introduces the current special journal issue *International Practices for Regenerating and Restoring Forest Trees by Seeding*, for which the concept and effort to undertake were motivated within the IUFRO Task Force on Transforming Forest Landscapes for Future Climates and Human Well-Being. The journal issue, comprised of contributions from North America, South America, Europe, Asia, and Oceania, represents a significant range of seeding activities inclusive of scores of species, forests, forestation sites, and climates. Approached as an information guide and source of advancements that are being studied and applied in contemporary practice around much of the globe, *International Practices for Regenerating and Restoring Forest Trees by Seeding* provides a synthesis of regional practice and research intended for an audience of early career scientists, practitioners, and policy makers working in forest restoration.

Keywords
forest restoration, forestation, forest degradation, direct seeding, artificial regeneration

Introduction to international practices for regenerating and restoring forest trees by seeding

Forestation is the process of establishing trees to create forest cover. Generally encompassing afforestation, reforestation, and forest restoration, forestation is accomplished through artificial regeneration practices or through practices that promote natural regeneration. However, the term has been most associated with approaches to create forest cover that involve artificial regeneration. Seeding, in the context of forestation, is a means of artificial regeneration in which plant seeds are distributed to propagate desired forest vegetation, particularly trees and shrubs (Deal 2018). While only two broad methods of seeding are recognized, broadcast and direct seeding (Table 1), a diversity of seeding approaches have been developed to initiate regeneration of sites where the natural regeneration process of desired species has been degraded such that it is limited or unlikely to occur. The promotion of naturally developing seedlings and forest structure, a broad applicability at all spatial scales, a relatively low cost, a high feasibility for regenerating remote sites, and a low operational intensity are among the favorable characteristics that coalesce to promote seeding as a promising means of artificial regeneration (Löf et al. 2019). Thus, there is currently marked potential for seeding to be a viable option for artificial regeneration within the global area of deforested and degraded forest landscapes.

Forest workers began adopting the use of seeding to regenerate deforested or degraded woodlands and forests several centuries ago. One of the earliest documented efforts to establish forests through seeding originated from Europe during the early 14th century and rudimentary systems to support seeding efforts appeared as early as the 15th century, much earlier than systems for planting seedlings (Harmer and Kerr 1995; Huth et al. 2017). In the ensuing centuries, the European population and its exploitation of forest resources grew rapidly—this prompted early policy aimed at mitigating forest loss that encouraged forest regeneration and more extensive use of seeding (Huth et al. 2017). During the 17th century, heightened forest exploitation and expansion of agriculture in Europe precipitated the concept of forest sustainability and initiated modern forestry (Huth et al. 2017). As the primary means of artificially establishing forest stands, seeding was foundational to the silvicultural systems being developed and applied to temper the forest exploitation sweeping through much of Europe (Huth et al. 2017). Seeding remained the primary means of artificial regeneration throughout much of Europe until the early 20th century when development of operational forestry led to advancement of regeneration methods based on planting seedlings (Huth et al. 2017; Löf et al. 2019; but see Harmer and Kerr (1995) regarding 17th century Great Britian).

Seeding eventually spread to other regions of the globe, for example, appearing in North America during the early 20th century (Toumey 1916). In most instances, it was introduced by practitioners faced with tremendous forest regeneration needs. In other words, practitioners were motivated by the search for a low-cost approach to artificial regeneration that could be adapted for the species and forests of interest and scaled for application to relatively large areas. In the case of North America, a wave of massive deforestation, e.g., millions of ha in the southern USA alone, was experienced across several regions of the continent when industrial lumbering swept across certain forested regions in the late 19th and early 20th centuries (Barnett 2014). Supported by comprehensive research to address the issue, operationally scaled successes with seeding conifers were realized in multiple regions of North America during the mid-20th century, e.g., pine (*Pinus* spp. L.) species in the southern region of the United States (1940s), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and other conifers in the Pacific Northwest region of the United States (1940s), and jack pine (*Pinus banksiana* Lamb.) in Ontario, Canada (1950s) (Scott 1970; Barnett 2014; Downer et al. 2024). Thus, seeding has historically been integral to large-scale forestation, persisting through time and across continents with the rise of modern forestry practices.

Contrary to the history of successes, forest establishment by means of seeding began to fall out of favor in many regions by the early 20th century. This can be attributed to multiple reasons including innovations that drove high success with planting seedlings in industrial reforestation operations. Additionally, contemporary application of seeding is often limited by biological, ecological, or practical constraints. These constraints, along with advancements in nursery culture, genetic improvement of nursery stock, and forestation practices, have solidified planting seedlings as the primary means of artificial regeneration in most operational settings. Though seeding usually demonstrates an initial cost advantage over planting seedlings, the more intensive and costly planting will usually demonstrate higher establishment success and

Table 1. Glossary of seeding terms[1].

Term	Definition
Seeding	The distribution of seed by hand, machine, or aerially in artificial regeneration (Deal 2018). Two methods of seeding are recognized, 1) **broadcast seeding** and 2) **direct seeding**. **Sowing** is synonymous with seeding.
Broadcast seeding	A method of seeding in which seeds are spread throughout an area onto the ground without incorporation into soil. Broadcast seeding can be accomplished through 1) **Hand seeding**, 2) **Machine seeding**, or 3) **Aerial seeding**. To broadcast seed by hand, workers walk systematically through the regeneration area casting seed with their hands or with a hand-held seed spreader. Broadcast seeding with a machine involves the use of a vehicle-drawn seeding implement or seed spreader. The type of vehicle used in the operation, e.g., draught animal, tractor, truck, off-road vehicle, or all-terrain vehicle, is determined by the size of the seeding area, the size of the seeding implement, and the terrain of the seeding area. Aerial seeding is accomplished with either crewed (e.g., helicopter) or uncrewed (e.g., **aerial drone**) vehicles equipped to carry and spread seed. Seed to be broadcasted is often mixed with an inert matrix (e.g., sand) or **pelleted** to improve flow through the seeding machine, trajectory of fall through the air, distribution on the ground, contact with soil, or probability of germination.
Direct seeding	A method of seeding that involves sowing seed into furrows or holes in soil, i.e., analogous to "planting" a seed. The furrows or holes are established to control the location and spacing of seed and subsequent seedlings on the regeneration site. Direct seeding can be accomplished through 1) **Hand Seeding** or 2) **Machine seeding**. To direct seed by hand, workers walk systematically through the regeneration area, create a small furrow or hole with a hand tool at the **sowing spot**, deposit seed in the furrow or hole, and cover the seed with soil dug to create the furrow or hole. **Machine seeding** involves the use of a seeding implement or planting drill drawn by a draught animal, tractor, truck, off-road vehicle, or all-terrain vehicle. Planting drills and seeding implements used for direct seeding are designed with coulters to create the furrows where seed is deposited and discs or packing wheels to cover the seed with soil and close the furrow. Advancements in development of **terrestrial drones** and **aerial drones** for direct seeding show promise for their use in the near future. **Drilling** is synonymous with direct seeding.
Drone seeding	Seeding, either broadcast or direct, accomplished with a **drone**. A drone is an uncrewed vehicle, either aerial or terrestrial, used to distribute seed. **Terrestrial drones** designed for seeding are typically autonomous planting machines for seed.
Line seeding	A variant of direct seeding in which seed is sown in linear furrows established across the forestation area.
Hydroseeding	A variant of broadcast seeding in which seed is mixed into a slurry of mulch and water then sprayed onto the regeneration site with hydraulic equipment.
Pneumatic seeding	A variant of broadcast seeding in which seed is blown onto the regeneration site with pneumatic equipment.
Precision seeding	Using GIS, sensors (e.g., LiDAR), and variable-rate technology to map microsites and plan and deliver seeding. Seeds are precisely placed at optimal depth and spacing or location, based on pre-sowing site maps. Precision seeding is especially useful for establishing mixtures and for seeding desirable microsites known to favor germination and seeding establishment.
Seed pelleting	Pelleting coats seeds with inert materials to render them uniform in size, shape, and weight, or to increase probability of germination. This process is especially useful for small or irregularly shaped seeds. Seeds are pelleted with coating materials (e.g., clay or seed treatments such as stimulants or protectants). **Seed encapsulation** or **coating** are synonymous with pelleting.
Seeding hole	A relatively large and deep hole that is dug for direct seeding on steep terrain or on highly erodible soils. Soil removed from the hole is often mixed with organic matter or fertilizers to prepare the seedbed and improve seedling rooting and growth.
Sowing spot	The precise location on a forestation site where a seed or seeds are sown when direct seeding.
Spot seeding	Sowing several seeds per sowing spot. Either broadcast seeding or direct seeding can be used for spot seeding.

[1] Growth and development of seeding efforts across the many forested regions of the world have introduced inconsistencies in terminology usage to the literature. Considering the range of manuscripts compiled and the intended user, the value of this journal issue as a resource to the practitioner and student hinges on consistent use of clearly defined terms. Table 1 presents a glossary that should clarify usage, reduce ambiguities, and enable the reader to appreciate relationships between terms applied throughout the issue.

rate of stand development (Grossnickle and Ivetić 2017). This is notably the case for species with seed traits that render them problematic for seeding, such as some light-seeded species and those with seed that show dormancy, sensitivity to desiccation, poor storage, or high susceptibility to depredation (Figure 1). Poor establishment success and relatively slow stand development also materialize when seeding high productivity sites with unchecked growth of competing vegetation. Indeed, issues like seed depredation and competing vegetation led 17th century English practitioners to concentrate seeding in small "garden" areas adjacent to the regeneration site where the effort could be protected and tended to produce seedlings for transplanting (Harmer and Kerr 1995). While early and present-day research advances have addressed some of the issues mentioned above, particularly for a locale or a region, many remain easier to overcome in a seedling nursery setting rather than a field setting.

Figure 1. A pedunculate oak seedling (*Quercus robur* L.) emerging from a prototype "seed tube" designed to protect seed from depredation and provide a favorable microenvironment to the germinant. (Photo credit: Magnus Löf).

Still, seeding has remained integral to contemporary forest regeneration prescriptions for some regions, forest types, site conditions, and forest management regimes (e.g., see Ivetić and Marinković (2026) in this issue for oak (*Quercus robur* L.) stand establishment in Serbia) and is regaining favor in forest restoration settings (e.g., large scale, remote sites where planting seedlings is not practical, where planting seedlings may be restricted by access or cost, where seeded species are used as framework species, or to enrich plantings for developing complex forest structure). In these settings, contemporary demands for seeding are pushing innovation to improve success, many of which are addressed in this journal issue.

Advances in research and application of seeding are improving today's forestation efforts by addressing a varied list of issues and inefficiencies encountered during operational seeding (Stanturf et al. 2024). New and improved seed delivery technologies represent an important source of advancements (Figure 2). For example, developments in aerial drone and drone-based sensor technologies have redefined how broadcast seeding is conducted in many regions while terrestrial and aerial drone-based platforms show promise for expanding precision seeding to favored microsites on large and remote forestation areas (Downer 2024; and see Castro et al. (2026) for seeding Mediterranean pines and Wang et al. (2026) for seeding *Pinus massoniana* Lamb. in China published in this issue). Too, engineering improvements to machine seeders are providing efficient and effective means to sow seed mixtures, e.g., mixtures of differently sized seeds for seeding former agricultural sites in New Zealand (see Lord and Moss-Mason (2026) in this issue for seeding in temperate New Zealand).

Fresh approaches to sourcing and harvesting seed also contribute to the recent advances that are improving seeding. In this respect, drone technologies are demonstrating utility for identifying source trees and monitoring fruit ripeness, and technological development is advancing towards seed harvesting capabilities which could be particularly useful in tropical regions where source trees can be widely dispersed and difficult to access (Stanturf et al. 2024). Better knowledge and protocols to ensure appropriate genetic sourcing for disease resistance, site suitability, climate adaption, or other issues (see Pansing and Tomback (2026) for seeding whitebark pine (*Pinus albicaulis* Engelm.) and Lord and Moss-Mason (2026) for temperate New Zealand in this issue), along with seed networks for inventorying and distributing seeds, such as those established in Brazil (see Engel et al. (2026) for seeding in Brazil in this issue), are safeguarding future forest health and ecological success along with addressing operational demands for seeding.

Further, advances that lessen barriers to establishment success and development of desired forest cover have been realized through novel technologies and approaches that protect seed, facilitate seedling establishment, and prepare and manage the forestation area. Refined seed technologies, such as coating or encapsulating seed in briquettes or balls that can improve seed distribution, reduce seed desiccation, reduce seed predation, and facilitate seedling growth, are supporting seed conservation by benefiting seedling establishment (see López-Barrera and Garcia-Hernández 2026) for seeding oaks (*Quercus* spp. L.) in Mexico, Sudrajat et al. (2026) for seeding in Indonesia, and Castro et al. (2026) for seeding Mediterranean pines in this issue). Seed supply limitations in some regions have also driven the development of more efficient strategies for sowing seeds, e.g., precision seeding of microsites known to have higher probabilities of establishment success (see Pansing and Tomback (2026) for seeding whitebark pine and Castro et al. (2026) for seeding Mediterranean pines in this issue). More thoughtful plantation design and application of improved site preparation and management practices that control invasive species, mitigate degraded soil and hydraulic functions, or minimize animal damage have increased successes in promoting development of desired forest cover and achieving improved ecological functions (see Engel et al. (2026) for seeding in Brazil, Gardiner and Stanturf (2026) for seeding bottomland oaks, and Löf et al. (2026) for seeding oak in southern Sweden in this issue) (Figure 3). Thus, recent progress in research and application has fostered the opportunity for greater use of seeding in forestation by improving establishment success on forestation sites, raising cost effectiveness of seeding operations, and ultimately improving ecological and economic sustainability on degraded and deforested sites.

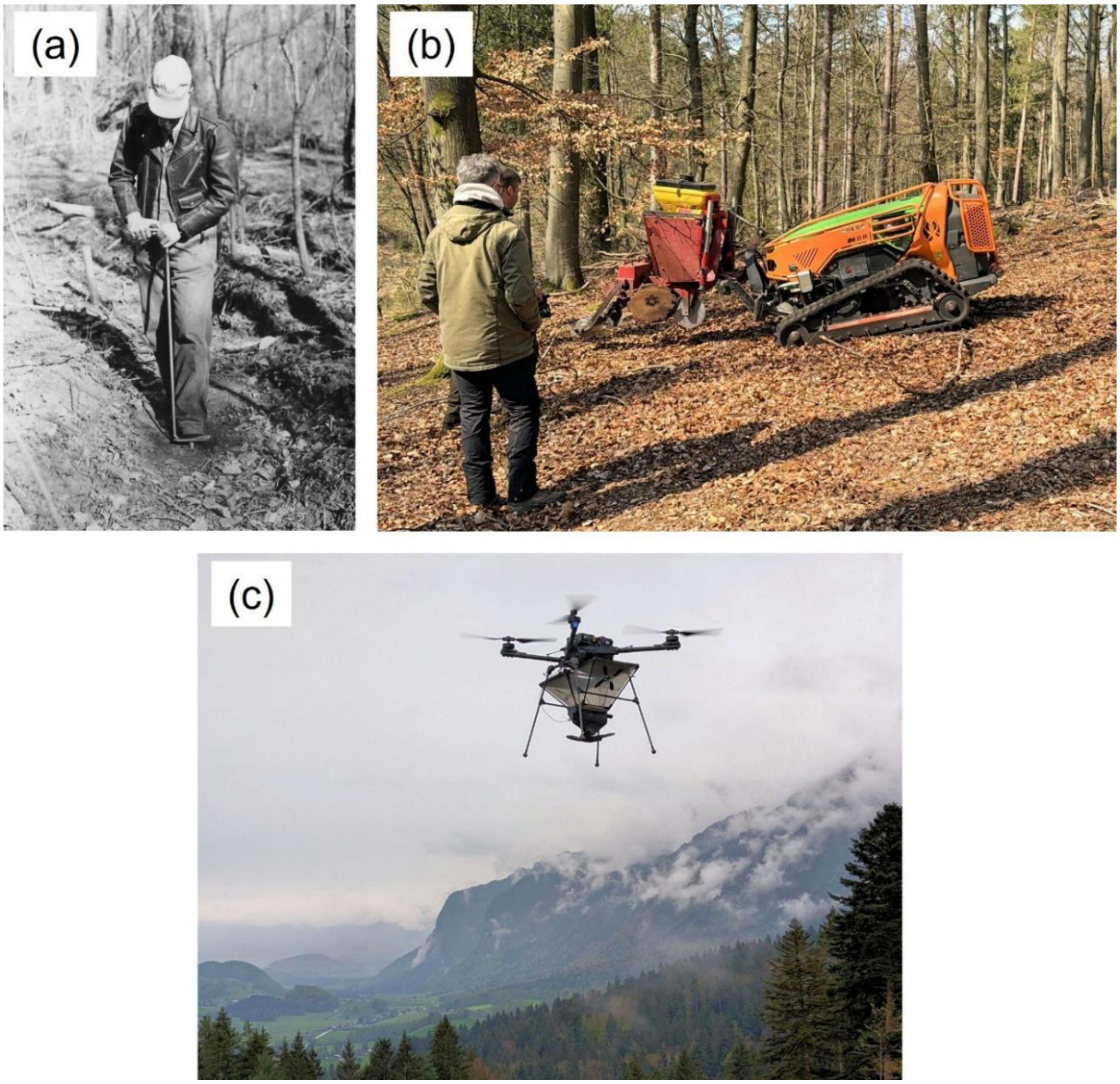

Figure 2. Advancement of seed delivery technologies: (a) a seeding tool used in the 1950s to create a small dimple in the soil surface for direct seeding bottomland oak (*Quercus* spp. L.) acorns, (b) a remotely controlled terrestrial rover used for direct seeding in degraded forest stands, (c) an aerial drone capable of broadcasting seed over relatively large and inaccessible sites. (Photo credits: (a) US Forest Service, Center for Bottomland Hardwoods Research, (b) Skyseed GmbH, Germany, (c) Skyseed GmbH, Germany).

The concept and effort to undertake this special journal issue was motivated within the IUFRO Task Force on Transforming Forest Landscapes for Future Climates and Human Well-Being. The intention was to produce a supplement to *Implementing Forest Landscape Restoration*, *A Practitioner's Guide*, which was published by IUFRO in 2017

(Stanturf et al. 2017). We approached this supplement as an information guide and source of advancements that are being studied and applied in contemporary practice around much of the globe. In this context, this issue on *International Practices for Regenerating and Restoring Forest Trees by Seeding* is intended to provide a synthesis of regional practice and research for an audience of early career scientists, practitioners, and policy makers working in forest restoration. Some contributed manuscripts are scoped by region or forest type, while others are species centric. Accordingly, manuscripts vary in length and detail, ranging from comprehensive syntheses to short case studies, depending on the level of development and use of seeding practices within the region or for the species of interest. Certainly, this journal issue is not inclusive of all seeding practices, either operational or experimental, being conducted across forest landscapes worldwide. Too, it was not our objective to discern the merits of seeding relative to the other means of active artificial forest regeneration, i.e., planting seedlings—others have begun laying the foundation to comprehensively approach this question (Lázaro-González et al. 2023). However, with contributions from North America, South America, Europe, Asia, and Oceania, it does represent a significant range of seeding activities inclusive of scores of species, forests, forestation sites, and climates. Thus, the substantial seeding expertise, knowledge, and practical experience captured in *International Practices for Regenerating and Restoring Forest Trees by Seeding* will provide the forest restoration community with a key resource for advancing global forest restoration.

Figure 3. European beech (*Fagus sylvatica* L.) seeded beneath a poplar (*Populus* spp. L.) plantation established on former agricultural land. This practice can be used to enrich fast-growing plantations with desired slower-growing species and increase forest structure complexity in forest restoration settings. (Photo credit: Palle Madsen).

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This paper may include research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All use of pesticides must be registered by appropriate agencies before they can be recommended.

CAUTION!

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

References

Barnett JP (2014) Direct seeding southern pines: history and status of a technique developed for restoring cutover forests. USDA Forest Service, Southern Research Station General Technical Report SRS-187, Asheville, NC, USA.

Castro J, Pérez-García M, Lovenstein H, Pedrini S (2026) Seeding pines in the Mediterranean region. Reforesta 21: 10-31. https://dx.doi.org/10.21750/REFOR.21.02.132

Deal RL (2018) The Dictionary of Forestry. Society of American Foresters, Bethesda, MD, USA.

Downer R, Manteuffel-Ross T, Tymon L, Aghai M (2024) Direct seeding for conifer regeneration in the Pacific Northwest: a past, present, and future of operational practices. J For 122:171–184. https://doi.org/10.1093/jofore/fvad050

Engel VL, de Souza DC, Parrotta J (2026) An overview of seeding methods to restore tropical forests of Brasil. Reforesta 21:105-145. https://dx.doi.org/10.21750/REFOR.21.07.137

Gardiner E, Stanturf J (2026) Seeding bottomland oaks (*Quercus* spp.) in the southern United States. Reforesta 21: 166-189. https://dx.doi.org/10.21750/REFOR.21.09.139

Grossnickle SC, Ivetić V (2017) Direct seeding in reforestation – a field performance review. Reforesta 4:94–142. https://doi.org/10.21750/REFOR.4.07.46

Harmer R, Kerr G (1995) Creating woodlands: to plant trees or not? In: Ferris-Kaan R (Ed.) The Ecology of Woodland Creation. John Wiley and Sons, Chichester, England.

Huth F, Wehnert A, Tiebel K, Wagner S (2017) Direct seeding of silver fir (*Abies alba* Mill.) to convert Norway spruce (*Picea abies* L.) forests in Europe: A review. For Ecol Manag 403:61–78. https://doi.org/10.1016/j.foreco.2017.08.017

Ivetić V, Marinković M (2026) Seeding to establish Ravni Srem oak forests, Nothern Serbia. Reforesta 21:199-207. https://dx.doi.org/10.21750/REFOR.21.11.141

Lázaro-González A, Andivia E, Hampe A, Hasegawa S, Marzano R, Santos AMC, Castro J, Leverkus AB (2023) Revegetation through seeding or planting: a worldwide systematic map. J Environ Manag 337:117713. https://doi.org/10.1016/j.jenvman.2023.117713

Löf M, Miles B, Moe KT, Pohl N, Schönbeck L (2026) Seeding of oak in southern Sweden. Reforesta 21: 190-198. https://dx.doi.org/10.21750/REFOR.21.10.140

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. For Ecol Manag 448:474–489. https://doi.org/10.1016/j.foreco.2019.06.032

López-Barrera F, García-Hernández MÁ (2026) Seeding acorns from montane cloud forest restoration in central Veracruz, Mexico: practical experiences. Reforesta 21:146-165. https://dx.doi.org/10.21750/REFOR.21.08.138

Lord J, Moss-Mason K (2026) Seeding for native afforestation in temperate New Zealand forests. Reforesta 21:68-86. https://dx.doi.org/10.21750/REFOR.21.05.135

Pansing E, Tomback D (2026) Seeding of whitebark pine (*Pinus albicaulis*) in western north American subalpine forests: Development and application. Reforesta 21:32-53. https://dx.doi.org/10.21750/REFOR.21.03.133

Scott JD (1970). Direct seeding in Ontario. For Chron 46:453–457.

Stanturf JA, Dumroese RK, Elliot S, Ivetić V, Khokthong W, Kleine M, Lang M, Löf M, Madsen P, Prescott C, Young T (2024). Advances in forest restoration management and technology. In: Katila P, Pierce Colfer CJ, de Jong W, Galloway G, Pacheco P, Winkel G (eds.) Restoring Forests and Trees for Sustainable Development: Policies, Practices, Impacts, and Ways Forward. Oxford Academic, New York, NY, USA, pp 297–334. https://doi.org/10.1093/9780197683958.003.0011

Stanturf J, Gardiner E (2026) Seeding forest trees. Reforesta 21:208-224. https://dx.doi.org/10.21750/REFOR.21.12.142

Stanturf J, Mansourian S, Kleine M, eds. (2017) Implementing Forest Landscape Restoration, A Practitioner’s Guide. International Union of Forest Research Organizations, Special Programme for Development of Capacities (IUFRO-SPDC), Vienna, Austria.

Sudrajat D, Yulianti, Rustam E (2026) Seeding of tropical tree species in Indonesia. Reforesta 21:87-104. https://dx.doi.org/10.21750/REFOR.21.06.136

Wang FC, Liu Q, Wang GG (2026) *Pinus massoniana* seeding practices for forest restoration in China. Reforesta 21:54-68. https://dx.doi.org/10.21750/REFOR.21.04.134

Toumey JW (1916) Seeding and Planting: A Manual for the Guidance of Forestry Students, Foresters, Nurserymen, Forest Owners, and Farmers. John Wiley & Sons, Inc., New York, NY, USA.

Seeding pines in the Mediterranean region

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Abstract

Extensive disturbance to the ecologically, socially, and economically important pine (*Pinus* spp. L.) forests of the Mediterranean region has created a strong need for forest restoration throughout the region. Seeding could potentially be a viable option for regenerating some of the 10 pine species that occur in the region, especially the fire-adapted serotinous species, but previous seeding efforts have been marked with inconsistent success. From our synthesis of available literature and practical experience, we briefly summarize the history of applied trials and pine seeding research, examine the factors that determine pine seeding success, and discuss what we have learned that can make seeding an ecologically and economically viable approach to pine forest establishment in the Mediterranean region. Future refinement of autonomous drones for seed delivery, selection of favorable sowing microsites, and improvement of seed coating technologies that minimize seed predation and support seedling establishment will support "precision restoration" practices that promise to advance pine seeding to an operational scale in the Mediterranean region.

Keywords

forest restoration, direct seeding, *Pinus* spp., precision restoration, seeding drones, seed coating

Contents

1 Introduction

Pine (*Pinus* spp. L.) forests in the Mediterranean region have experienced extensive disturbance due to human activities, including excessive logging, overgrazing, and fire. There is a need to restore many of these forests, as pines are a major component of Mediterranean region forests and have high ecological, social, and economic relevance (Moreira et al. 2012; Ne'eman and Osem 2021). A heterogeneous set of pine species grow naturally in the Mediterranean region with very different biogeographical origin and ecology. In this chapter, we follow the criteria of Grivet and Olsson (2021), who considered ten species with "a native distribution range extending to the Mediterranean region and which grow under a Mediterranean climate" (Figure 1, Table 1). Overall, in the Mediterranean region these pines are distributed from sea level to ca. 2500 m elevation (Table 1). Some of the species show clear Mediterranean-type characteristics, such as adaptation to fire (e.g., serotinous cones) or high drought resistance (e.g., *P. halepensis* Mill. and *P. brutia* Ten.) relative to other pines, while others show typical boreo-alpine traits such as high cold resistance and low drought resistance (e.g., *P. sylvestris* L. and *P. mugo* Turra) (Table 1). Seed mass of the different species varies by 80 times, from ca. 7.5 mg in *P. sylvestris* and *P. mugo* to 600 mg in *P. pinea* L. Finally, there are striking differences between species in morphological and functional traits including root/shoot ratio, control of stomatal aperture, water potential, or photochemical efficiency. These traits, which determine seedling size, water uptake, and growth rate, underlie species adaptation to environmental conditions and are key for seeding success under drought stress (Matías et al. 2017; Salazar-Tortosa et al. 2018a,b; Salazar-Tortosa et al. 2020), and, subsequently, the regeneration capacity of the various species that inhabit the region.

Table 1. Pines that inhabit the Mediterranean region and some of their characteristics relevant to revegetation through seeding. Data on seed mass are the average of the entries listed in the Supplementary Information of Salazar-Tortosa et al. 2020, which were extracted from available databases or published articles and reports except for *P. uncinata* Ramond ex D.C.; for *P. uncinata*, seed mass was obtained from Notivol et al. 2012. Information about serotiny is extracted from Salazar-Tortosa et al. 2020 (Supplementary Information Table S2). Drought tolerance and frost resistance are broadly defined in relative terms across the species. Elevational ranges sourced from Boydak 2004 (‡), San-Miguel-Ayanz et al. 2016 (†), AEMA 2008 (*), and Franco 1986 (**).

Species	Main distribution; species silvics; and habitat characteristics	Elevational range (m)	Seed mass (mg)	Serotiny
***P. brutia* Ten. (Turkish pine)**	Mediterranean; Drought tolerant and fast growing; Low elevation and coastal areas	0–1500‡	45.7	Yes
***P. canariensis* C.Sm. ex D.C. (Canary island pine)**	Canary Islands (endemic); Resprouts after fire from epicormic buds; Volcanic slopes between 700 and 1200 m.a.s.l.	1200–1800*	102.4	Yes
***P. halepensis* Mill. (Aleppo pine)**	Mediterranean; Drought tolerant and fast growing; Low elevation to intermediate elevation, very common in coastal areas	0–2000†	25.7	Yes
***P. heldreichii* H.Christ (Bosnian pine)**	Mediterranean, small distribution in southern Italy and the Balkan peninsula; From intermediate elevation to high Mediterranean mountain areas, where it can reach the tree line	900–1800*	22.5	No
***P. mugo* Turra (dwarf mountain pine)**	Frost resistant, drought intolerant, and slow growing; Alpine, high mountain habitats, pine that reaches the highest elevation in the Mediterranean region	200–2700†	7.6	No

P. nigra **J.F.Arnold (black pine)**	Mediterranean; Drought intolerant and fast growing; Moderate elevation to high Mediterranean mountain areas where it can form part of the timberline	800–1500†	19.8	No
P. pinaster **Aiton (maritime pine)**	Mediterranean; Drought resistant and fast growing; Temperate to warm locations, inhabiting from coastal areas to moderate elevation	0–2000†	55.6	Yes
P. pinea **L. (stone pine)**	Mediterranean; Drought resistant and cold sensitive, wingless seed; Mostly in coastal areas, very common in sandy soils and on dunes	0–1000**	600.4	No
P. sylvestris **L. (Scots pine)**	Frost resistant, drought intolerant, and slow growing; Boreo-alpine, high Mediterranean mountains where it forms part of the timberline.	0–2600†	7.6	No
P. uncinata **(mountain pine) Ramond ex D.C.**	Frost resistant, drought intolerant, and slow growing; High European mountains where it forms the timberline.	600–2400†	9	No

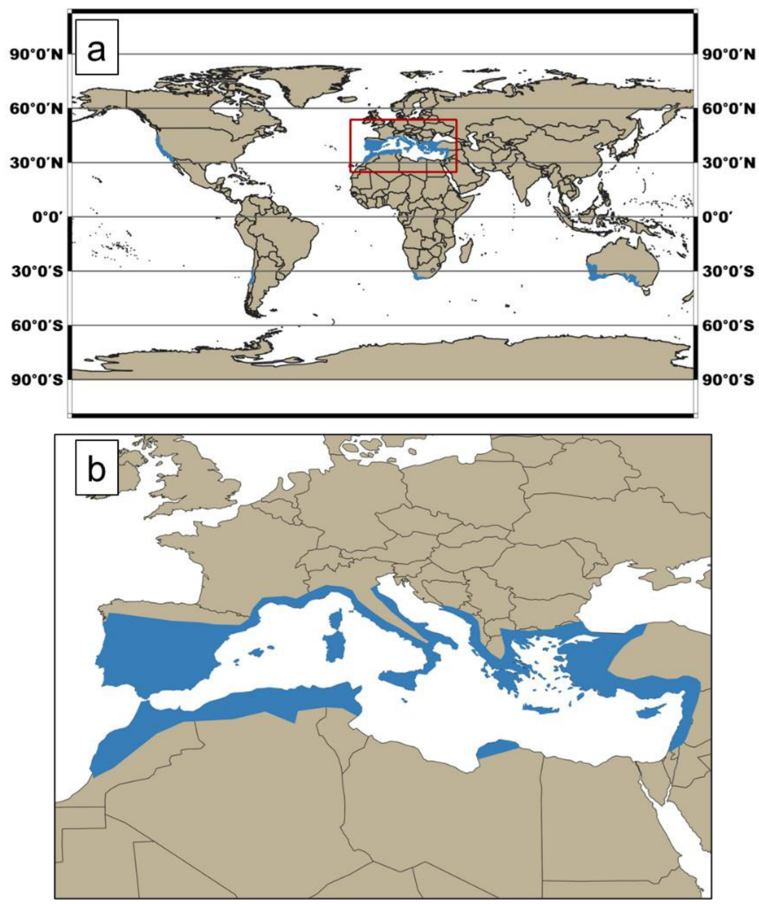

Figure 1. (a) Regions of the world with Mediterranean-type ecosystems (in blue); and (b) distribution of Mediterranean-type ecosystems in the Mediterranean basin. The climate of the Mediterranean region is characterized by low to moderate rainfall but with a hot and dry summer that imposes strong drought conditions on plants. Redrawn from Rundel et al. (2016).

Pine regeneration via seeding should be feasible at least for some species. This is substantiated by many examples of high natural pine recruitment from seed after wildfire. In the case of serotinous pines, seedling densities can often approach several thousand ha^{-1} after wildfire (e.g., Calvo et al. 2013; Hibsher et al. 2013). Moreover, pine seeding has been done with great success in some cases, particularly in dunes and other sandy areas, as relayed through oral communications, local reports, or journals by personnel of local forest districts—though often difficult to access, these sources provide information of high ecological and forestry value (e.g., Cueto 2001) (Figure 2). The challenge to make sowing seeds an efficient method for restoration of pine forests in the Mediterranean basin is, therefore, to understand the bottlenecks for seedling recruitment for the various species and to apply the most appropriate practices and technologies to overcome these barriers. In this sense, practices exist today to protect seed from biotic and abiotic stresses and to select the most suitable microsites for improving sowing efficiency. In the following sections, we describe the success of pine seeding relative to seedling recruitment in the Mediterranean region, the main environmental factors that determine this success, and suggest several ways to improve the feasibility of seeding as a reforestation method for pine forest restoration in this region.

Figure 2. Seeding of stone pine (*P. pinea* L.) in sand dune reforestation in Doñana National and Natural Park, southern Spain (year 2022). The central plant was planted as a 1-year-old. The plants at each side of the central seedling resulted from sowing one seed at each spot at the same time as seedling planting. Pine reforestation via direct seeding, sowing the seed in soil, has been successful in many cases, particularly in sand dunes, although there are scant academic reports (Photo credits: Óscar Pérula, Plant-for-the-Planet foundation).

2 Low success rate reported in the literature

As a starting point we need to define what is regarded as success in pine seeding for reforestation or forest restoration. The most basic measure of success is determined by the proportion of seedlings or saplings established from a given number of seeds (hereafter recruitment success). Many other ecological, economic, or social considerations should also be considered, such as the development of ecosystem structure and function, resilience, biodiversity, ecosystem services, or various socio-ecological aspects including the emotional engagement by the local population to the restored forest and the economic benefits it may bring to them. Nonetheless, to set the issue to the most basic definition, we only consider recruitment success in this chapter. In this sense, pine seeding success is evaluated as a seedling recruitment percentage that reduces the economic and ecological costs (this can be monetized in a single index) of planting nursery raised seedlings (hereafter seedling outplanting), which currently is the most used reforestation technique (Lázaro-González et al. 2023). Furthermore, success may differ from one site to another depending on expectations. For example, we might set a higher expectation for recruitment success in environments or biomes with mild summer stress than in others with strong summer stress, as observed across the Mediterranean region. In addition, an even distribution of recruited seedlings would be more important for establishing production forests than for restoring forests holding a conservation objective.

We frame recruitment success for this chapter with a goal of establishing resilient forests with a structure that will promote natural succession. Under this criterion, we consider recruitment success of 2.5% at the sapling stage an acceptable baseline, i.e., a minimum of 250 saplings from seeding 10,000 seed ha^{-1}. This may not be considered a success for other biomes or objectives, e.g., regeneration of productive stands, but it can be in the context of restoring functional forests with a main aim of the provision of ecosystem services and biodiversity conservation.

A maximum of 10,000 seed ha^{-1} is also critical to our assessment. The amount of seed used in seeding operations today is extremely high (often above 100,000 ha^{-1}) as it is expected that many seeds or seedlings will be lost to seed predation, failure to germinate, mortality during seedling emergence, or mortality during establishment. High sowing rates are a clear disadvantage as compared to planting nursery-grown seedlings, because of the size and vigor of planting stock. Seed collection and preparation is often the costliest part of a pine seeding operation (see section on Making Seeding a Viable Approach), and therefore, measures to reduce seeding density ha^{-1} will positively impact seeding efficiency. Additionally, procuring large quantities of seed can be problematical if local seed availability is low—this can move seed provisioning to non-local sources that consequently can threaten indigenous genetic diversity and local adaptation of populations (Mohan et al. 2021; Castro et al. 2024). Thus, it is imperative to reduce sowing rates for seeding to be a scalable alternative to other afforestation or reforestation practices.

Under these criteria, we can state that the overall success of seeding to regenerate pine forests in Mediterranean ecosystems is low (Table 2). For example, Ordoñez et al. (2004) sowed *P. nigra* J.F. Arnold seed over the soil surface at 111,111 seed ha^{-1} and obtained 0% regeneration in open habitats and shrublands. Espelta et al. (2003), who broadcasted 25,000 *P. nigra* seed ha^{-1}, observed between 0 to 200 seedlings ha^{-1} after two years (recruitment success of 0.8% in the best case). J. Castro (unpublished data) conducted an experimental sowing of *P. sylvestris* in relict forests in southern Spain by broadcasting 100,000 seed ha^{-1}, and seedling recruitment after the first growing season was 0% (climatic conditions were very adverse because of drought). The company DroneCoria (Spain) conducted aerial drone seeding (10,000 seed ha^{-1}) of *P. halepensis* across several hectares in a semi-arid region of SE Spain (Supplementary Material in Castro et al. 2024). Again, recruitment success was 0% after one year, even though *P. halepensis* grows naturally in the area and very often regenerates abundantly after fire (climatic conditions were also particularly dry in this case).

Some positive results are also reported, but mostly from reports of various forest districts or other administrations, not peer-reviewed journals. Despite the value of these reports, this information is difficult to track. Moreover, these reports should be considered with caution because they are often not supported by an experimental design that would allow one to draw unequivocal conclusions about establishment success, as very often neither seeding density nor seedling density are properly controlled. Still, some academic studies report good or acceptable recruitment success from seeding, with recruitment values around 5% after several years and sometimes considerably higher (Table 2). However, most of these works are designed to disentangle factors that determine seedling establishment, not necessarily results that can be applied at large spatial scales. For example, it is common for seeds to be buried about 1 cm deep in these studies, a measure that reduces seed predation and improves germination (see section on Factors that Determine Pine Seeding Success). Additionally, it is common in these studies to protect sown seeds from predators with measures such as wire cages (Table 2). This is done to ensure seedlings will be present to study in subsequent phases of the research. Such control of environmental factors is usually infeasible for large-scale forest restoration, but this knowledge provides direction for improving pine seeding success.

Table 2. Compilation of studies showing data of pine seedling establishment across different environmental conditions, including habitats, microhabitats, sowing method, soil conditions, or experimental manipulation such as predator exclusion or irrigation. The inclusion of studies does not follow a systematic search; rather, it seeks to include a wide representation of different conditions. Ys = years of study. Emrg. = Seedling emergence. Seed was sown at ≈ 1 cm below the soil surface in all cases where seed was buried. Succ. = seedling survival at the end of the study; survival refers either to the percentage of seedlings that survived from those registered as emerged (*), or the percentage of seedlings recruited from sown seed (†), depending on the data available in each study; the values for recruitment have been calculated in some cases if they were expressed in other terms, e.g., seedlings ha^{-1} divided by seed sown ha^{-1}. The data refers to the time expressed in column Ys. For data extraction from figures, we used WebPlotDigitizer 4.7. Precip. = annual precipitation. Pred. = predators.

Ref.	Ys	Species	Location and environmental conditions	Seeding details (when buried, at ≈ 1 cm in all cases)	Emrg. (%)	Succ. (%)	Highlighted comments
Bladé and Vallejo 2008	2	*P. halepensis* Mill.	Spain, burnt pine forest. Semiarid. Precip. ≈ 640 mm	Buried, intact soil. Pred. excluded. Data are average values for all the experimental plots and families (maternal trees)	71.7	48.6*	A clear example of *P. halepensis* regeneration success with seeding, but pred. excluded, and seeds buried.
Castro et al. 2002a	3	*P. sylvestris* L.	Spain, mountain meadows. Precip. ≈ 830 mm	Buried with 3 soil treatments: intact (meadow), clipped vegetation, and scarified soil. Pred. not excluded	≈25	1.2*	Ca. 1.2% survival in all the treatments. Seedling emergence is possible without pred. exclusion if seeds are buried
Castro et al. 2002a	<1	*P. sylvestris* L.	Spain, mountain meadows. Precip. ≈ 830 mm	Surface, pred. not excluded, the same treatments indicated above Surface, intact soil (meadow) + pred. excluded Surface, clipped veg. (meadow) + pred. excluded Surface, scarified soil + pred. excluded	0–0.8 6.4 17.2 55.5		Pred. block regeneration if seeds are on the surface. Soil scarification boost emergence. (Survival not monitored in this study).
Castro et al. 2004	4	*P. sylvestris* L.	Spain, native forests.	Buried, intact soil in bare ground + pred. excluded	49.2 50.8	2.4* 8.2*	*Juniperus communis* acts as a nurse plant for seedling recruitment

			Precip. ≈ 830 mm	Buried, intact soil under *Juniperus* + pred. excluded			
Castro et al. 2004	3	*P. sylvestris* L.	Spain, shrublands. Precip. ≈ 830 mm	Buried, intact soil in bare ground. Pred. not excluded	28.7	0*	*Salvia* acts as a nurse plant for seedling recruitment. Emergence is possible without pred. exclusion if seeds are buried
				Buried, intact soil under *Salvia*. Pred. not excluded	41.7	4.2*	
Castro et al. 2005	2	*P. sylvestris* L.	Spain, native forests. Precip. ≈ 830 mm	Buried, intact soil in bare ground. Pred. excluded	25.4	8.9†	Shrubs act as nurse plants for seedling recruitment. Summer drought reduction with irrigation boost seedling establishment
				Buried, intact soil under shrubs. Pred. excluded	60.8	9.7†	
				Buried, intact soil in bare ground. Pred. excluded + irrigation	24.9	12.7†	
				Buried, intact soil under shrubs. Pred. excluded + irrig.	67.8	32.2†	
Espelta et al. 2003	2	*P. nigra* J.F.Arnold	Spain, burnt areas. Precip. ≈ 600 mm.	Spot seeding. Not indicated if buried or surface. Two soil treatments: grazed and prescribed burning. Chemical repellent for insects and birds.		0.6† in all cases	Recalculated from original data. Not successful
García-Morote et al. 2017	2	*P. halepensis* Mill.	Spain, burnt areas. Semiarid. Precip. ≈ 332 mm	Buried in scarified soil. Pred. not excluded	5.8	0.2†	A cover of wood chips increased soil moisture and seedling recruitment. Aspect (N or S-facing) had no effect
				Buried in scarified soil + wood chips cover. Pred. not excluded	18.2	4.6†	
Martínez-García et al. 2018	5	*P. nigra* J.F.Arnold	Spain, burnt areas. Precip. ≈ 647 mm	Buried, 2 soil treatments: intact soil and scarified soil. Pred. not excluded. South facing slopes	45.8	0*	Seedling emergence is possible without pred. exclusion if seeds are buried. Seedling survival in locations with reduced water stress (north-facing slopes). Woodchips had little effect (not included in these data).
				Buried, 2 soil treatments: intact soil and scarified soil. Pred. not excluded. North facing slopes	44.2	7.5*	
Nackhoul et al. 2020	0.5	*P. pinea* L.	Lebanon, mature pine stand. Precip. ≈ 964 mm	Buried slightly. Intact soil (with pine litter)	48	Ca. 0	The exclusion of pred. had no effect in this study.
				Buried slightly, scarified soil, Pred. excluded	64	Ca. 0	
Tíscar et al. 2017	3	*P. pinaster* Aiton *P. nigra* J.F.Arnold *P. sylvestris* L.	Spain, different elevations; data for the lowest value of basal area. Precip. ≈ 765mm	Buried, intact soil (but litter removed). Pred. excluded Buried, intact soil (but litter removed) + water addition (similar to Castro et al. 2005). Pred. excluded.	70–90	0–40*	Seedling emergence very high when litter is removed and seed are buried. Drought reduction boost seedling establishment (ca. 3 times higher in irrigated plots).
Espelta et al. 2003	2	*P.nigra* J.F.Arnold	Spain, burnt areas. Precip. ≈ 600 mm	Broadcast (manual) 25,000 seeds ha^{-1} in different treatments, including intact soil. Pred. not excluded	–	<0.8†	Recalculated from original data. Not successful
Fernandes et al. 2017	<1	*P. pinaster* Aiton	Portugal, two sites of the Atlantic coast: Precip. ≈ 944 mm (wetter and cooler) and Precip. ≈ 735 mm (drier and hotter)	Broadcast in 1 x 1 m experimental plots at a density of 600,000 seeds ha^{-1}. Scarified soil, pred. not excluded. • Wetter site: • Drier site:	≈12 ≈10	≈26* ≈5*	Summer drought reduction boost seedling establishment. Data reported are the average of different treatments in shrubland habitats (recalculated from original).

Ordóñez et al. 2004	<1	*P. nigra* J.F.Arnold	Spain, different habitats. Precip. ≈ 725 mm	Broadcast in 3 x 3 m experimental plots at a density of 111,111 seeds ha^{-1}. Habitats: bare soil, short grasses and shrublands. Pred. not excluded.	0	–	Seedling establishment happened below the canopy of the pine forest, but this habitat does not need restoration.
Taboada et al. 2017	3	*P. pinaster* Aiton	Spain, burnt areas. Precip. up to 900 mm	Broadcast in contour lines with a portable shoulder spreader at ≈ 25000 seeds ha^{-1}. Pred. not excluded.	–	24†	6000 seedlings ha^{-1}. However, the effect of previous seed bank not controlled. A resampling 5 y after controlling seed bank offers no effect.

3 Factors that determine pine seeding success in the Mediterranean region

In general, pine regeneration via seeding in the Mediterranean region is constrained by four fundamental factors: seed predation, drought stress (mostly summer drought), non-contact with mineral soil, and weed competition.

3.1 Seed predation

Seeds of the Mediterranean pines are consumed by birds, mammals, and insects, e.g., ants (Family Formicidae) and beetles (Order Coleoptera) (Castro et al. 1999; Espelta et al. 2003) (Figure 3), with rates that can reach almost 100% of seed availability (Castro et al. 1999; Lucas-Borja et al. 2010; Ziffer-Berger et al. 2017; and references therein). Therefore, measures that reduce seed predation will be advantageous for pine seeding. Seed burial clearly reduces loss to predators (Castro et al. 2002a; Martínez-García et al. 2018) (Table 2), which is a general fact across species. Seed burial also boosts germination, and thus, it is a method with cumulative advantages for seeding. However, it is difficult to implement seed burial with broadcast techniques and especially with aerial seeding, so seed burial is largely restricted to ground-based operations. In cases where seed remains exposed on the surface, alternatives are to coat seed with substances that either repel predators or camouflage their appearance, smell, or both (Figure 3; also see section on Seed Coating to Improve Pine Recruitment Success). Ongoing research on these technologies holds promise for advancing seeding as a useful and scalable restoration method (Pedrini et al. 2020).

Methods to reduce predation may be combined to increase their efficiency. For example, capsaicin (the spicy molecule in chili pepper (*Capsicum* spp. L.) deters mammals but is ineffective against birds. Thus, we may treat seed with capsaicin if they are to be spot seeded under shrub nurse plants (see below for information concerning nurse plants). This is because rodent (Order Rodentia) activity increases under shrubs, where they find protection from their own predators. Some avian seed predators may not venture below shrubs, presumably because their movements would be restricted and their probability of escaping predation compromised (this is, in any case, a supposition to be tested). Thus, predation by two seed predator guilds may be reduced by seeding capsaicin-treated seed under nurse shrubs. Similarly, the timing of seeding can be critical to the level of seed predation sustained. For example, the high seedling density that often occurs after fires for species bearing serotinous cones may be due to the combined effects of the ashes camouflaging seed and the reduced density of predators such as rodents and insects (many seed predators will die or be displaced during the fire and the site will not be recolonized for several months (Retana et al. 2012)). Post-fire restoration via sowing seed should be conducted shortly (within months) after the fire to reduce the effect of seed predators, and ideally during a period of rain.

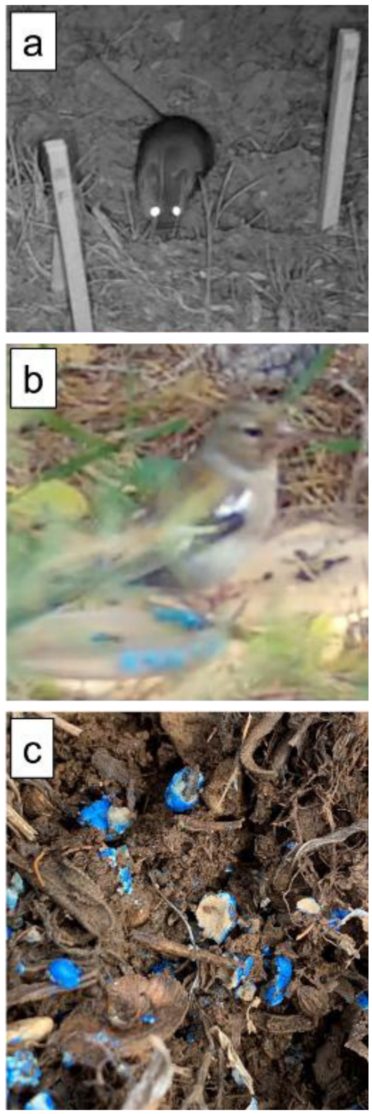

Figure 3. Rodents and birds are the main predators of pine seeds in the Mediterranean region. (a) A wood mouse (*Apodemus sylvaticus*) feeding on Scots pine (*P. sylvestris* L.) seed in Sierra Nevada National Park (Granada, Spain); seed coated with 4 different deterrent substances were scattered onto the soil surface. (b) A common chaffinch (*Fringilla coelebs*) is offered seed of Aleppo pine (*P. halepensis* Mill.) in the mountainous area close to the seashore in Granada (Spain). The control (non-coated) seed (petri dish on right) were predated unlike the seed coated with Bitrex (bitter substance) dissolved in a blue dye (petri dish on left). It is postulated that the color blue is not noticed by some birds. (c) A blue coating and Bitrex did not prevent seed predation by the wood mouse in Sierra Nevada National Park. Presented data are preliminary (Castro et al. unpublished) (Photo credits: Jorge Castro).

3.2 Drought stress

Pine seedling mortality from drought, in particular summer drought, can be very high in the Mediterranean region. The stress of drought may be considered the main factor of seedling mortality with values that usually range between 70–95% depending on the species, often reaching 100% after the first year (Espelta et al. 2003; Castro et al. 2004; Nackhoul et al. 2020). The situation may get even worse under current climate change scenarios, which is an increase in aridity that may impact regeneration capacity and distribution of pine species in the region (Salazar-Tortosa et al. 2024). Accordingly, any measure to reduce summer drought stress could help seedling establishment resulting from seeding operations. For example, mitigation of summer drought with irrigation that simulates a mild summer is a measure that has consistently resulted in positive effects on regeneration for various species, multiplying recruitment success by a factor of 2 to 3 (Castro et al. 2005 and Tíscar et al. 2017 in Table 2; see also Ruano et al. 2009; Mendoza et al. 2009; Matías et al. 2012 for similar results). However, irrigating seedlings will not be feasible in most restoration cases, especially in remote areas. Nonetheless, the risk of summer drought stress can be reduced in other ways. For example, we may consider the landscape (macro) when prioritizing seeding efforts—Martínez-García et al. (2018) obtained 7.5% seedling survival for *P. nigra* on north-facing slopes in contrast to 0% on south-facing slopes (Table 2).

Site selection for pine seeding in the Mediterranean region should also consider a smaller spatial scale, i.e., the microhabitat. Several studies have consistently reported the beneficial effect of nurse plants on regeneration of many tree species, particularly pines in the Mediterranean region (Castro et al. 2004; Boulant et al. 2008; Petrou and Milios 2012) (Table 2). As a result, it is common to observe a clear association of pine seedlings and saplings with successional shrubby species (Figure 4). Shrubs reduce radiation, evaporation, and thus heat stress (Castro et al. 2002b). They also enhance water availability by directing stem flow from rain intercepted by branches and foliage to soil, by hydraulic lifting, or by reducing surface runoff (Tromble 1988; Muller et al. 2018) that facilitates water infiltration in microhabitats. The latter aspect is further enhanced by soil porosity which is improved by the root system of the shrub. Soil moisture availability is further retained by leaf litter from the shrub, reducing evaporative losses. Both leaf litter and (decaying) roots also contribute to soil organic matter which positively impacts soil water retention and soil nutrient status.

Biological legacies such as burnt logs or branches remaining after fires can be important microhabitat. These biological legacies can provide nurse structures that reduce drought and heat stress, trap water runoff, and provide nutrients and organic matter, all together improving pine seedling recruitment (Castro 2021). Also, shrubs and biological legacies may protect seedlings from large herbivores (Figure 4) thereby facilitating pine recruitment (Castro 2021). The use of shrubs as nurse plants or biological legacies as nurse structures is likely the most necessary measure for increasing success of pine seeding in Mediterranean environments. Some benefits provided by shrubs may be replicated by mulching with woodchips, i.e., layered mulch on top of the sown seed. For example, García-Morote et al. (2017) found that recruitment success increased from 0.2% to 4.4% when seeds of *P. halepensis* were covered with a layer of woodchips, in accordance with a common positive effect of mulching on seedling establishment across many species due to increased moisture, reduced weed competition, temperature buffering, and nutrient supply (Jonas et al.

2019; Lucas-Borja et al. 2020). Additionally, seed can be coated with a hydrogel to further improve moisture retention after sowing (Section 4).

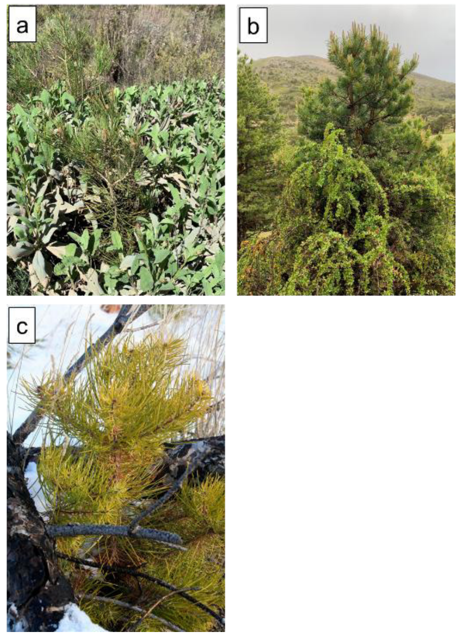

Figure 4. A common situation in Mediterranean ecosystems is the recruitment of tree species facilitated by nurse shrubs that improve microclimatic conditions, particularly by reducing drought stress during the summer. Because they are vulnerable to drought, pine seedling mortality can be substantial in summer. (a) Two individual Aleppo pine (*P. halepensis* Mill.) trees recruiting within the canopy of a salvia plant (*Salvia oxyodon* Webb & Heldr.) in a semiarid environment (Albacete, southeastern Spain). (b) Scots pine (*P. sylvestris* L.) sapling growing within a spiny shrub (*Berberis hispanica* Boiss. & Reut.) in Sierra de Baza, southern Spain. (c) A seedling of maritime pine (*P. pinaster* Aiton) recruiting in a burnt area: biological relics, dead branches after the fire, serve as nurse structures providing favorable microclimatic conditions (moderating irradiation and desiccating winds) without competing for water (Sierra Nevada National Park, southern Spain) (Photo credits: Jorge Castro).

Favorable microhabitats may also include small depressions or simple soil pits where surface runoff accumulates after a rain event (Evenari et al. 1971). This concept is mimicked by soil scarification prior to seeding, which breaks soil crusts that restrict rainwater infiltration. For drought prone areas, customized seed drills are integrated with V-shaped scalping blades or discs that create a weed-free strip and collect surface runoff in the seeded line (Whyte 2003). Seeded lines should preferably follow contour lines of the site to trap surface runoff without inducing gully erosion. The seeding implement is drawn behind a four-wheel drive vehicle or tractor, so it is restricted to flat or undulating terrain without too many rocks.

Finally, we may select the most appropriate sowing times for seed germination and plant establishment, for example, during periods of expected rainfall (as far as these periods fall within the period of seed germination), reducing the residence time of seeds during which they are vulnerable to seed predation. In summary, there is a suite of practices to alleviate drought stress; these focus on soil moisture conservation by reducing evaporational losses and increasing water availability next to seeds. Their effectiveness can be further improved in combination with other interventions. For example, seed coated with hydrogel can be sown under nurse shrubs and buried in the ground.

3.3 Seed contact with mineral soil and weed competition

Seed contact with mineral soil is essential. If the seed remains on a layer of organic matter, such as leaf litter or a layer of herbaceous plants, germination is still possible. However, the radicle will likely desiccate before reaching mineral soil and the seedling will die prematurely (Castro et al. 2002a) (see summary in Table 2). This differs in respect to pine seeding in other biomes where soil moisture is higher during the germination period. In drier regions, direct seeding (burying or pressing seeds in the ground) is particularly expected to be more successful than broadcasting seed. Germination of broadcasted seed may be improved by scarifying the soil surface, e.g., using disc or tine harrows, prior to seeding to facilitate seed burial or contact with mineral soil (Nackhoul et al. 2020; Rautio et al. 2023), especially in the presence of a soil crust or weed cover. Overall, site preparation such as soil scarification or scalping will increase the probability of seeding success due to higher water infiltration, reduced competition with herbaceous vegetation, or increased contact of the radicle with mineral soil (e.g., Castro et al. 2002a; Nakhoul et al. 2020). These measures can be effective even if applied at a small spatial scale, localized where the seed will be sown, which will minimize negative impacts of soil disturbance across the entire site.

The impact of the surface organic layer will also depend on seed mass. We may expect that the larger the seed, and thus, the more nutrients and energy it contains, the more likely the radicle will reach mineral soil. This is supported by Nackhoul et al. (2020), who found seedling emergence by *P. pinea*, the species with the largest seed mass in the Mediterranean region, was reduced if seed were sown on unscarified soil, but these seed still reached a relatively high (48%) emergence percentage (Table 2). These observations contrast markedly with those for small-seeded species like *P. sylvestris* (Castro et al. 2002a) (Table 2), suggesting that establishment of small-seeded species will particularly benefit from soil scarification, scalping, or seed burial (to aid contact of the seed with mineral soil).

Competition from weeds, especially dense herbaceous vegetation, also reduces pine seedling recruitment and growth (Castro et al. 2002a; Castro and Leverkus 2019). It is thus advisable to scalp soil or simply avoid areas where herbaceous vegetation has become too dense. Alternatively, as noted earlier, nurse shrubs can reduce herbaceous weed competition, providing a suitable microhabitat for seeding.

4 Seed coating to promote pine recruitment success

Because seed predation and seedling mortality caused by summer drought are the main limitations to pine seeding success in the Mediterranean region, any measure to alleviate the negative effects of these factors will increase the probability of success. As stated above, a common practice for achieving this objective is seed coating.

Seed coating consists of applying layers of beneficial materials through an accretion process to the seed coat. Coating seed modifies the physical traits (size, weight) of the seed and delivers substances that help the seed endure environmental stress or avoid predation. Coatings that provide protection against predators or pathogens, or promote germination and establishment are most common (Pedrini et al. 2017; Pearson et al. 2019). Coating pine seed is particularly feasible and easy given their size, shape, and lack of external appendices (except the wing, which is easily removed) (Benkman 1995). Coating seed is especially beneficial to mechanical seeding, either terrestrial broadcasting or aerial seeding, because they can be transformed into a spherical structure of desired diameter to facilitate spreading (Figure 5). Also, seed coating could be particularly useful for aerial seeding with drones (see below). This is because coating can be used to improve the ballistic properties of seeds, allowing them to fall to the ground with more predictable trajectories that are less influenced by wind and turbulent air currents (Domaradzki et. al. 2012).

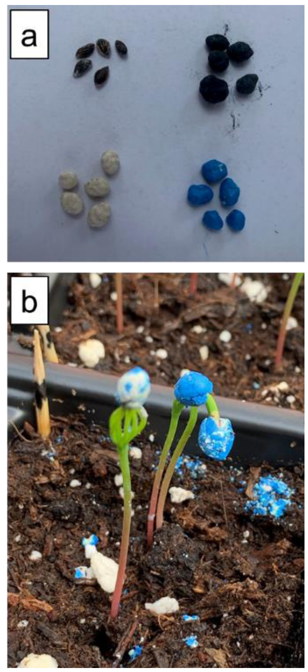

Figure 5. (a) Coating Aleppo pine (*P. halepensis* Mill.) seed. Natural seed (upper left), seed coated with active carbon (upper right), coated with neem oil (bottom left), and coated with bitrex plus a blue dye (bottom right). (b) A greenhouse experiment to test the effect of coatings on seed germination and seedling emergence (Photo credits: Jorge Castro).

A key feature of seed coating is the ability to load the artificial coating with substances designed to deter seed predation. For example, coloring the external surface of the seed coat blue was enough to limit predation by some bird species (Pawlina et al. 1996) (Figure 5). While this practice can work on predators that rely on vision, it may not work on rodents that rely heavily on taste and smell (Figure 3c). A primary problem with deterring substances is that their effect is often not consistent across sites. The extent of protection given by repellents may depend on factors such as the nutritional quality of seed, the species depredating the seed, or the availability of alternative foods (Nolte and Barnett 2000). As a result, some repellents show positive effects in some cases but no effect in others. For example, Bitrex (denatonium benzoate), an extremely bitter chemical compound, has sometimes reduced seed predation by rodents. However, in an ongoing experiment conducted by the authors, preliminary results indicate that Bitrex did not provide protection against predation by the wood mouse (*Apodemus sylvaticus*) (Figure 3c). Another approach reported to be effective is to mask the smell of seed with material such as activated carbon (Taylor et al. 2020). However, in the above-mentioned experiments, activated carbon did not seem to protect *P. sylvestris* seed from predation by the wood mouse (Castro et al. unpublished data).

Seed coating can also be used to promote seed germination and seedling survival. For example, we can add super-absorbent hydrogels that attract and retain water to the proximity of the seed and provide extra water during periods of drought (Amirkhani et al. 2023). Surfactants (or wetting agents) have also been used on hydrophobic soils to allow water to infiltrate soil right under the seed. This seed treatment can be particularly relevant in improving germination and emergence in post-wildfire reforestation. Coating seed with nutrients has also been evaluated but the delivery of macronutrients (NPK) often proved detrimental because of damage to the extending radicle (Scott 1989). Application of trace elements has proven effective in supplementing missing micro-nutrients. Other coating additives have been tested to promote seed germination, such as gibberellic acid to overcome dormancy (Larson et al. 2023), activated carbon to provide protection from herbicides (Davies et al. 2024), and salicylic acid to improve survival under stress conditions (Pedrini et al. 2021), though these have not yet been tested on pine seeds. Clearly, more research is needed to find effective seed coating practices that improve protection and promote pine establishment and recruitment in restoration settings.

5 Making seeding a viable approach for pine forest restoration in the Mediterranean basin

Seeding success is determined by three main, inter-related factors: (1) increase the recruitment probability associated with each seed, (2) reduce sowing density, and (3) reduce cost of seeding while limiting impact to the ecosystem (Castro et al. 2024). An action that meets any of these conditions will make seeding more competitive with planting seedlings and more viable as a restoration approach. We propose several options that meet these conditions. All strategies may use coated seed as described in Section 4, as this contributes to restoration success and facilitates the use of mechanical devices.

Direct seeding or spot seeding, burying seeds in the ground, is probably the best option to increase recruitment success while reducing the amount of seed needed (e.g., Table 2). Sowing can be done manually, including hand-operated seeders, allowing seeds to be easily inserted at the desired depth. Manual seeding also facilitates precision placement of seed at selected microsites, for example underneath shrubs. Because of early seedling mortality, it can be prudent to sow multiple seed per spot. Seed could be dispensed separately at the same spot or within a single pellet containing several seeds (agglomerate).

Direct seeding could also be done with terrestrial seeding robots that are currently being developed by companies like Land Life (Amsterdam, The Netherlands; Figure 6a). Terrestrial seeding robots can integrate spot-wise site preparation and sowing by scalping to remove weeds, exposing the mineral soil before burying seeds or seed pellets and creating a small depression to trap rainwater (Figure 6b). Considering their limited weight and spot-level operation, seeding robots are environmentally less intrusive than conventional terrestrial seeding methods that use heavy machinery to scarify soil or pull seeding lines. Seeding robots may operate in fleets covering large parcels of land, including moderately inclined, rugged, and rocky terrain, cumbersome for operation of conventional seeding machinery. The fully controlled seeding process addresses variation in microhabitat conditions regarding natural shelter, soil conditions including aspect and rainwater entrapment, and can enable precision seeding near nurse shrubs.

In the absence of nurse shrubs, microsite conditions can be improved artificially by using biopolymer based mini-protectors, i.e., shuttles (©Land Life, 2024) (Figure 7a). Shuttles are partly pushed into the soil to provide above- and belowground protection against seed predation and to provide shelter against high irradiation and desiccating winds. In the driest environments, an additional disc-shaped structure, composed of biodegradable pulp fiber, can be affixed onto the soil surface around the shuttle (Figure 7b). This device reduces evaporation from soil and suppresses weed competition, while water captured from rain events is channeled to the seed. Additional cardboard-based sleeves can be fixed on above-ground spike structures to further reduce light and drought stress, while providing extra protection against seed predation and browsing (Figure 7c). Considering the additional investment, shuttles should preferably protect multiple seeds to realize cost effective recruitment (Figure 7d).

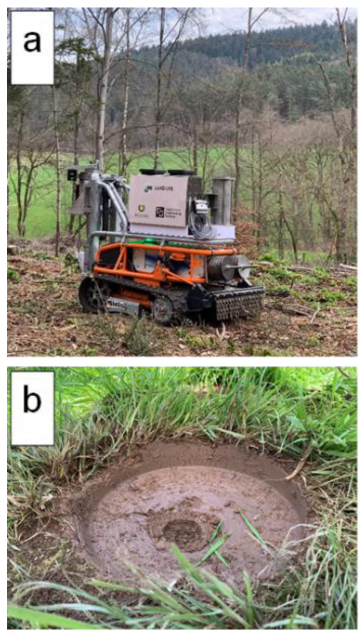

Figure 6. Terrestrial seeding robot developed by Land Life Company BV (Amsterdam, The Netherlands). (a) Prototype of a seeding unit mounted onto an electrically powered mobile platform enabling spot seeding particularly under rugged terrain conditions. (b) Detail of scarified soil spot prior to seeding: exposing mineral soil by eliminating weed cover, while its conical shape traps rainwater favoring soil moisture retention (Photo credits: Land Life Company BV).

Aerial seeding using conventional methods like airplanes or helicopters appears ineffective in the Mediterranean region. Even if coated seed are used to reduce seed predation, conventional aerial seeding places most seeds on microsites unsuitable for germination (e.g., dense weed cover, hard soil crust). Because pine recruitment success in the Mediterranean region relies enormously on favorable microhabitat selection, aerial seeding based on current drone technology should be considered. Drones can place seed in preferred microhabitats with favorable moisture and aspect conditions and can methodically avoid areas with dense herbaceous cover at small spatial scales. Also, drones may place seed in preselected microsites at sub-meter scale, for example, under nurse shrubs—an application termed "precision drone seeding" (Castro et al. 2024) (Figure 8). This method can markedly reduce the number of seed required and, hence, the operational cost can be reduced up to 6–7 times in respect to traditional seedling planting (Castro et al. 2024). Drone seeding could, therefore, be useful and competitive if the paradigm were changed from broadcast seeding the entire site to be restored to precision drone seeding that delivered seed to the most suitable microsites for establishment (Castro et al. 2024). This procedure could be further automated with the use of artificial intelligence that incorporates high resolution remote-sensing imagery and algorithms that recognize the best microsites for seed deployment at the sub-meter scale, e.g., specific nurse shrubs (Castro et al. 2024). Unlike terrestrial seeding, drone seeding can be deployed on particularly steep terrain with poor access where large areas can be seeded in a short period of time, broadening the scalability of reforestation. However, soil preparation and seed burial, two factors that clearly increase seeding success, cannot be addressed by seeding with drones.

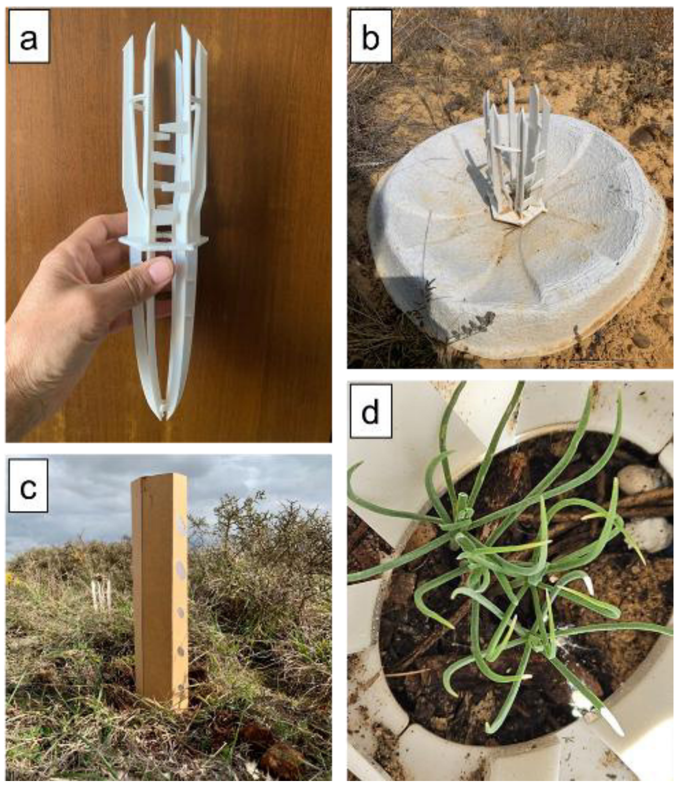

Figure 7. Shuttle technology developed for seeding or planting by Land Life Company BV (Amsterdam, The Netherlands). (a) The shuttle is inserted in the ground to the middle flange, the device provides above- and belowground protection against birds, browsers, and rodents, while the upper part improves microclimatic conditions by providing shelter against high irradiation and desiccating winds. Under more challenging drought conditions shuttles may be combined with a rainwater harvesting disc (b), which also controls weeds, and a top sleeve (c) providing more shelter to support germination and early seedling establishment. Several seeds can be sown per shuttle to ensure recruitment success (d); in the picture, four Scots pine (*P. sylvestris* L.) seedlings plus two non-germinated, coated seeds (Photo credits: Land Life Company BV).

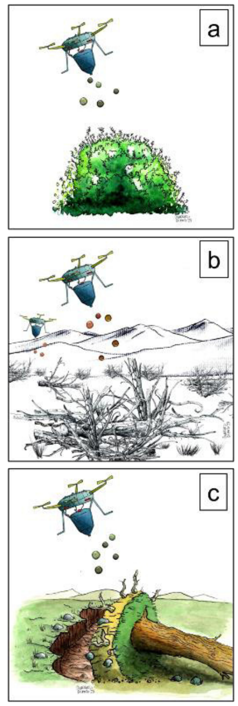

Figure 8. Examples of potential uses of drone seeding at the sub-meter scale. (a) Nurse shrubs provide favorable microclimatic conditions for seedling establishment and protection against herbivory. (b) Biological legacies such as piles of branches left after post-fire management can act as nurse structures. (c) Microtopographic features such as pits and mounds left by fallen trees after windstorms create favorable ecological niches where seedling establishment could have greater success. Drones can drop seed in these particular microsites using a precision-seeding approach. The process can be automated with the use of high-resolution remote sensing imagery and artificial intelligence. Reproduced from Castro et al. 2024.

6 Conclusions

Pine seeding is an afforestation and reforestation method that has generally showed low success in the harsh environmental conditions of the Mediterranean region. Results for seeding are typically much more unpredictable than planting in terms of reforestation success. Additionally, successful cases of pine reforestation with seeding usually employed a large amount of seed per hectare, which could create problems of seed supply and scalability. These are the most likely reasons that seeding has been used much less commonly than seedling outplanting. Nonetheless, seeding has been demonstrated to be a feasible and successful method of forest restoration in some cases for the Mediterranean region.

Building on past successes, pine seeding may become more successful and increasingly efficient as a restoration approach through incorporation of new technologies with traditional methods and ecological knowledge under the paradigm of “precision restoration” (Castro et al. 2021). In this respect, development of effective and efficient seed coating technologies to deter seed predators and increase seedling establishment are needed. We also must become more proficient in selecting the best locations to sow seed, even at sub-meter scale (microhabitats), and factoring potential hazards that the seedlings will face through recruitment, e.g., herbivory. Seed should ideally be sown in the ground. This increases the cost of the operation but can substantially increase establishment success, particularly if seed is placed below nurse shrubs. Aerial seeding with drones and terrestrial seeding robots may help to scale pine seeding beyond what can be achieved with conventional technologies and should be a main focus for future research.

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8 References

AEMA (2008) Agencia Europea de Medio Ambiente. Tipología de bosques europeos. https://www.miteco.gob.es/content/dam/miteco/es/calidad-y-evaluacion-ambiental/publicaciones/TipologiaBosquesEuropeos_tcm30-185660.pdf (last accessed 23 November 2024).

Amirkhani M, Mayton H, Loos M, Taylor A (2023) Development of superabsorbent polymer (SAP) seed coating technology to enhance germination and stand establishment in red clover cover crop. Agronomy 13(2):438. https://doi.org/10.3390/agronomy13020438

Benkman CW (1995) Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. Oikos 73:221–224. https://doi.org/10.2307/3545911

Bladé C, Vallejo R (2008) Seed mass effects on performance of *Pinus halepensis* Mill. seedlings sown after fire. For Ecol Manag 255:2362–2372. https://doi.org/10.1016/j.foreco.2007.12.039

Boulant N, Navas ML, Corcket E, Lepart J (2008) Habitat amelioration and associational defence as main facilitative mechanisms in Mediterranean grasslands grazed by domestic livestock. Écoscience 15:407–415. https://doi.org/10.2980/15-3-3126

Boydak, M (2004) Silvicultural characteristics and natural regeneration of *Pinus brutia* Ten.—a review. Plant Ecol 171:153–163.

Calvo L, Torres O, Valbuena L, Luis-Calabuig E (2013) Recruitment and early growth of *Pinus pinaster* seedlings over five years after a wildfire in NW Spain. For Syst 22(3):582–586. http://dx.doi.org/10.5424/fs/2013223-04623

Castro J (2021) Chapter 25 - Post-fire restoration of Mediterranean pine forests. In: Ne'eman G, Osem Y (eds) Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer Nature Switzerland AG, Cham, Switzerland, pp 537–565. https://doi.org/10.1007/978-3-030-63625-8

Castro J, Gómez JM, García D, Zamora R, Hódar JA (1999) Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecol 145:115–123. https://doi.org/10.1023/A:1009865703906

Castro J, Zamora R, Hódar J (2002a) Mechanisms blocking *Pinus sylvestris* colonization of Mediterranean mountains meadows. J Veg Sci 13:725–731. https://doi.org/10.1111/j.1654-1103.2002.tb02100.x

Castro J, Zamora R, Hódar JA, Gómez JM (2002b) Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restor Ecol 10:297–305. https://doi.org/10.1046/j.1526-100X.2002.01022.x

Castro J, Zamora R, Hódar J A, Gómez J M (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. J Ecol 92(2):266–277. https://doi.org/10.1111/j.0022-0477.2004.00870.x

Castro J, Zamora R, Hódar J A, Gómez J M (2005) Alleviation of summer drought boosts establishment success of *Pinus sylvestris* in a Mediterranean mountain: An experimental approach. Plant Ecol 181:191–202. https://doi.org/10.1007/s11258-005-6626-5

Castro J, Leverkus AB (2019) Effect of herbaceous layer interference on the post-fire regeneration of a serotinous pine (*Pinus pinaster* Aiton) across two seedling ages. Forests 10:74. https://doi.org/10.3390/f10010074

Castro J, Morales-Rueda F, Navarro FB, Löf M, Vacchiano G, Alcaraz-Segura D (2021) Precision restoration: a necessary approach to foster forest recovery in the 21st century. Restor Ecol 29(7):e13421. https://doi.org/10.1111/rec.13421

Castro J, Alcaraz-Segura D, Baltzer JL, Amorós L, Morales-Rueda F, Tabik S (2024) Automated precise seeding with drones and artificial intelligence: a workflow. Restor Ecol 32(5):e14164. https://doi.org/10.1111/rec.14164

Cueto M (2001) Ordenaciones de pinares de pino piñonero en la provincia de Cádiz. Cuadernos de la Sociedad Española de Ciencias Forestales 11:125–134.

Davies KW, Clenet DR, Madsen MD, Brown VS, Ritchie AL, Svejcar LN (2024) Activated carbon seed technologies: Innovative solutions to assist in the restoration and revegetation of invaded drylands. J Environ Manag 371:123281. https://doi.org/10.1016/j.jenvman.2024.123281

Domaradzki M, Kaniewska J, Weiner W (2012) The application of agglomerative granulation for seeds. Part 2. Pelleting of organic seeds. Chemik 66:473–478.

Espelta JM, Retana J, Habrouk A (2003) An economic and ecological multi-criteria evaluation of reforestation methods to recover burned *Pinus nigra* forests in NE Spain. For Ecol Manag 180:185–198. https://doi.org/10.1016/S0378-1127(02)00599-6

Evenari M, Shanan L, Tadmor N (1971) The Negev, the Challenge of a Desert. Harvard University Press, Cambridge, MA, USA.

Fernandes P, Máguas C, Correia O (2017) Combined effects of climate, habitat, and disturbance on seedling establishment of *Pinus pinaster* and *Eucalyptus globulus*. Plant Ecol 218(5):501–515. https://doi.org/10.1007/s11258-017-0706-1

Franco JDA (1986) *Pinus*. In: Castroviejo S, Laínz M, López-González G, Montserrat P, Muñoz-Garmendia F, Paiva J, Villar L (eds) Flora Ibérica, vol. I. Real Jardín Botánico, CSIC, Madrid, Spain, pp 168–174.

García-Morote FA, Martínez-García E, Andrés-Abellán M, Caballero ER, Miettinen H, López-Serrano FR (2017) Direct seeding of *Pinus halepensis* Mill. for recovery of burned semi-arid forests: Implications for post-fire management for improving natural regeneration. Forests 8(9):353. https://doi.org/10.3390/f8090353

Grivet D, Olsson S (2021) Chapter 1 - Phylogenies and evolution of Mediterranean pines. In: Ne'eman G, Osem Y (eds) Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer Nature Switzerland AG, Cham, Switzerland, pp 3–17. https://doi.org/10.1007/978-3-030-63625-8

Hibsher N, Moshe Y, Bney-Moshe E, Ben-Moshe E, Zangi E, Zuck A, Osem Y (2013) Post-fire regeneration in Mediterranean reforested sites as affected by mechanical site preparation—lessons for restoration. Appl Veg Sci 16:629–639. https://doi.org/10.1111/avsc.12030

Jonas JL, Berryman E, Wolk B, Morgan P, Robichaud PR (2019) Post-fire wood mulch for reducing erosion potential increases tree seedlings with few impacts on understory plants and soil nitrogen. For Ecol Manag 453:117567. https://doi.org/10.1016/j.foreco.2019.117567

Larson AJS, Cartwright MM, Jones WD, Luce K, Chen M-Y, Petersen K, Nelson SV, Michaelis DJ, Madsen MD (2023) Slow release of GA_3 hormone from polymer coating overcomes seed dormancy and improves germination. Plants 12(24):4139. https://doi.org/10.3390/plants12244139

Lázaro-González A, Andivia E, Hampe A, Hasegawa S, Marzano R, Santos AMC, Castro J, Leverkus AB (2023) Revegetation through seeding or planting: A worldwide systematic map. J Environ Manag 337:117713. https://doi.org/10.1016/j.jenvman.2023.117713

Lucas-Borja ME, Silva-Santos P, Fonseca TF, Tíscar-Oliver PA, López-Serrano FR, Andrés-Abellán M, Martínez-García E, del Cerro-Barja A (2010) Modelling Spanish black pine postdispersal seed predation in Central-eastern Spain. For Syst 19(3):393–403.

Lucas-Borja ME, Plaza-Álvarez PA, González-Romero J, Miralles I, Sagra J, Molina-Peña E, Mora D, de las Heras J, Fernández C (2020) Post-wildfire straw mulching and salvage logging affects initial pine seedling density and growth in two Mediterranean contrasting climatic areas in Spain. For Ecol Manag 474:118363. https://doi.org/10.1016/j.foreco.2020.118363

Martínez-García E, Miettinen H, Rubio E, García-Morote FA, Andrés-Abellán M, López-Serrano FR (2018) Effects of post-fire management practices and slope-aspect on medium-term Spanish black pine regeneration: implications of using a direct seeding strategy in burnt areas. European J For Res 137(4):527–540. https://doi.org/10.1007/s10342-018-1121-4

Matías L, Castro J, Villar-Salvador P, Quero JL, Jump AS (2017) Differential impact of hotter drought on seedling performance of five ecologically distinct pine species. Plant Ecol 218:201–212. https://doi.org/10.1007/s11258-016-0677-7

Matías L, Zamora R, Castro J (2012) Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community. Oecologia 169:833–844. https://doi.org/10.1007/s00442-011-2234-3

Mendoza I, Zamora R, Castro J (2009) A seeding experiment for testing tree-community recruitment under variable environments: implications for forest regeneration and conservation in Mediterranean habitats. Biol Conserv 149:1491–1499. https://doi.org/10.1016/j.biocon.2009.02.018

Mohan M, Richardson G, Gopan G, Aghai MM, Bajaj S, Galgamuwa GA, Vastaranta M, Arachchige PSP, Amorós L, Corte APD, de-Miguel S, Leite RV, Kganyago M, Broadbent EN, Doaemo W, Shorab MAB, Cardil A (2021) UAV-supported forest regeneration: current trends, challenges and implications. Remote Sens 13(13):2596. https://doi.org/10.3390/rs13132596

Moreira F, Arianoutsou M, Corona P, De las Heras J (eds) (2012) Post-fire management and restoration of southern European forests. Springer, Dordrecht, The Netherlands.

Muler AL, van Etten EJB, Stock WD, Howard K, Froend RH (2018) Can hydraulically redistributed water assist surrounding seedlings during summer drought? Oecologia 187:625–641. https://doi.org/10.1007/s00442-018-4158-7

Nakhoul J, Santonja M, Fernandez C, Greff S, Bousquet-Mélou A, Dupouyet S, Nemer N, Kattar S, Abboud J, Prévosto B (2020) Soil scarification favors natural regeneration of *Pinus pinea* in Lebanon forests: Evidences from field and laboratory experiments. For Ecol Manag 459:117840. https://doi.org/10.1016/j.foreco.2019.117840

Ne'eman G, Osem Y (eds) (2021) Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer Nature Switzerland AG, Cham, Switzerland.

Nolte DL, Barnett JP (2000) A repellent to reduce mouse damage to longleaf pine seed. Int Biodeterior Biodegrad 45:169–174. https://doi.org/10.1016/S0964-8305(00)00060-3

Notivol E, Oliet JA, Serrada R (2012) *Pinus uncinata* Ram. In: Pemán JG, Navarro RM, Nicolás JL, Prada MA, Serrada R (eds), Producción y Manejo de Semillas y Plantas Forestales. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, Spain, pp 1003–1018.

Ordóñez JL, Franco S, Retana J (2004) Limitation of the recruitment of *Pinus nigra* in a gradient of post-fire environmental conditions. Écoscience 11:296–304. https://doi.org/10.1080/11956860.2004.11682836

Pawlina IM, Proulx G (1996) Study of house sparrow (*Passer domesticus*) feeding preference to natural color and guard coat blue coated seeds. Crop Prot 15:143–146. https://doi.org/10.1016/0261-2194(95)00087-9

Pearson DE, Valliant M, Carlson C, Thelen GC, Ortega YK, Orrock JL, Madsen MD (2019) Spicing up restoration: can chili peppers improve restoration seeding by reducing seed predation? Restor Ecol 27:254–260. https://doi.org/10.1111/rec.12862

Pedrini S, Merritt DJ, Stevens J, Dixon K (2017) Seed coating: Science or marketing spin? Trends Plant Sci 22:106–116. https://doi.org/10.1016/j.tplants.2016.11.002

Pedrini S, Balestrazzi A, Madsen MD, Bhalsing K, Hardegree SP, Dixon KW, Kildisheva OA (2020) Seed enhancement: getting seeds restoration-ready. Restor Ecol 28(S3):266–275. https://doi.org/10.1111/rec.13184

Pedrini S, Stevens JC, Dixon KW (2021) Seed encrusting with salicylic acid: A novel approach to improve establishment of grass species in ecological restoration. PLOS ONE 16:e0242035. https://doi.org/10.1371/journal.pone.0242035

Petrou P, Milios E (2012) Establishment and survival of *Pinus brutia* Ten*.* seedlings over the first growing season in abandoned fields in central Cyprus. Plant Biosyst 146:522–533. https://doi.org/10.1080/11263504.2011.633574

Rautio P, Hallikainen V, Valkonen S, Karjalainen J, Puttonen P, Bergsten U, Winsa H, Hyppönen M (2023) Manipulating overstory density and mineral soil exposure for optimal natural regeneration of Scots pine. For Ecol Manag 539:120996. https://doi.org/10.1016/j.foreco.2023.120996

Retana J, Arnan X, Arianoutsou M, Barbati A, Kazanis D, Rodrigo A (2012) Chapter 7 - Post-fire management of non-serotinous pine forests. In: Moreira F, Arianoutsou M, Corona P, De las Heras J (eds) Post-fire management and restoration of southern European forests. Springer, Dordrecht, The Netherlands, pp 151–170.

Ruano I, Pando V, Bravo F (2009) How do light and water influence *Pinus pinaster* Ait*.* germination and early development*?* For Ecol Manag 258:2647–2653. https://doi.org/10.1016/j.foreco.2009.09.027

Rundel PW, Arroyo MT, Cowling RM, Keeley JE, Lamont BB, Vargas P (2016) Mediterranean biomes: Evolution of their vegetation, floras, and climate. Annu Rev Ecol Evol Syst 47(1):383–407. https://doi.org/10.1146/annurev-ecolsys-121415-032330

Salazar-Tortosa D, Castro J, de Casas RR, Viñegla B, Sánchez-Cañete EP, Villar-Salvador P (2018a) Gas exchange at whole plant level shows that a less conservative water use is linked to a higher performance in three ecologically distinct pine species. Environ Res Lett 13:045004. https://doi.org/10.1088/1748-9326/aab18f

Salazar-Tortosa D, Castro J, Villar-Salvador P, Viñegla B, Matías L, Michelsen A, de Casas RR, Querejeta I (2018b) The "isohydric trap": a proposed feed-back between water shortage, stomatal regulation and nutrient acquisition drives differential growth and survival of European pines under climatic dryness. Glob Chang Biol 24:4069–4083. https://doi.org/10.1111/gcb.14311

Salazar-Tortosa D, Castro J, Saladin B, Zimmermann NE, Rubio de Casas R (2020) Arid environments select for larger seeds in pines (*Pinus* spp). Evol Ecol 34:11–26. https://doi.org/10.1007/s10682-019-10016-1

Salazar-Tortosa D, Saladin B, Castro J, Rubio de Casas R (2024) Climate change is predicted to impact the global distribution and richness of pines (genus *Pinus*) by 2070. Divers Distrib 30(7):e13849. https://doi.org/10.1111/ddi.13849

San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds) (2016) European atlas of forest tree species. Publication Office of the European Union, Luxembourg. https://doi.org/10.2788/038466

Scott JM (1989) Seed coatings and treatments and their effects on plant establishment. Adv Agron 42:43–83. https://doi.org/10.1016/S0065-2113(08)60523-4

Taboada A, Tárrega R, Marcos E, Valbuena L, Suárez-Seoane S, Calvo L (2017) Fire recurrence and emergency post-fire management influence seedling recruitment and growth by altering plant interactions in fire-prone ecosystems. For Ecol Manag 402:63–75. https://doi.org/10.1016/j.foreco.2017.07.029

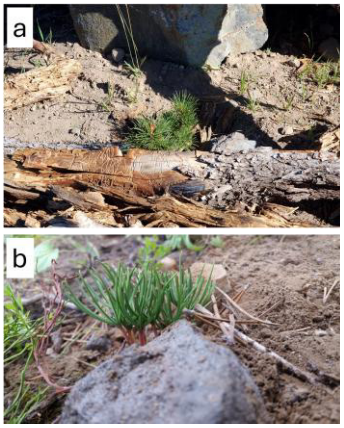
Taylor JB, Cass KL, Armond DN, Madsen MD, Pearson DE, St Clair SB (2020) Deterring rodent seed-predation using seed-coating technologies. Restor Ecol 28:927–936. https://doi.org/10.1111/rec.13158

Tíscar PA, Candel-Pérez D, Estrany J, Balandier P, Gómez R, Lucas-Borja ME (2017) Regeneration of three pine species in a Mediterranean forest: A study to test predictions from species distribution models under changing climates. Sci Total Environ 584–585:78–87. https://doi.org/10.1016/j.scitotenv.2017.01.150

Tromble JM (1987) Water interception by two arid land shrubs. J Arid Environ 15:65–70. https://doi.org/10.1016/S0140-1963(18)31005-X

Whyte S (2003) Revegetation techniques - a guide for establishing native vegetation in Victoria. Greening Australia Victoria, Victoria, Australia.

Ziffer-Berger J, Weisberg PJ, Cablk ME, Moshe Y, Osem Y (2017) Shrubs facilitate pine colonization by controlling seed predation in dry Mediterranean dwarf shrublands. J Arid Environ 147:34–39. https://doi.org/10.1016/j.jaridenv.2017.07.012



Seeding of whitebark pine (*Pinus albicaulis*) in western north American subalpine forests: Development and application

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Abstract

The rapid decline of whitebark pine (*Pinus albicaulis* Engelm.), a keystone species of upper subalpine and treeline elevational zones across many of the higher mountains of the western United States and Canada, has prompted the development of restoration strategies and practical restoration applications. Whitebark pine has been federally listed as 'threatened' in the United States, which elevates the restoration imperative. Seeding potentially provides a low-cost means of establishing the species in remote areas with limited access and/or land use constraints, but this restoration tool still lacks sufficient advancement to ensure operational success. We present an overview of whitebark pine ecology, outline the factors leading to its decline, summarize ongoing conservation efforts and restoration strategies, and review the available literature on seeding whitebark pine to identify barriers that challenge successful operationalization. Informing and advancing land management for conservation of whitebark pine will require refining seeding protocols by monitoring and reporting on trials to mitigate the main barriers to this application. Additional research is required to reduce seed pilferage by rodents, improve sowing techniques, identify favorable sowing microsites for improved seeding outcomes, and develop a reliable supply chain for seed resistant to introduced disease.

Keywords

whitebark pine, forest restoration, direct seeding, Clark's nutcracker, seed pilferage

Contents

1 Whitebark pine distribution, ecology, and ecosystem services

Whitebark pine (*Pinus albicaulis* Engelm.), an ecologically important species in rapid decline (Figure 1a), inhabits the upper subalpine and treeline elevational zones across many of the higher mountains of the western United States and Canada (Arno and Hoff 1990; McCaughey and Schmidt 2001; Olgilvie 1990). About 88% of whitebark pine's range in the United States occurs on federal (public) lands managed by the U.S. Forest Service, National Park Service, and Bureau of Land Management; and in Canada, whitebark pine occurs primarily on federal and provincial lands (COSEWIC 2010; U.S. Fish and Wildlife Service 2021). Indigenous lands in both nations comprise a portion of the whitebark pine distribution. The rapid decline of whitebark pine populations, especially in the northern Rocky Mountains, has been of management concern for more than 25 years (Tomback et al. 2001a), leading to multiple regional and range-wide restoration strategies and plans, as well as the development of restoration tools and applications, including seeding (Tomback et al. 2022).

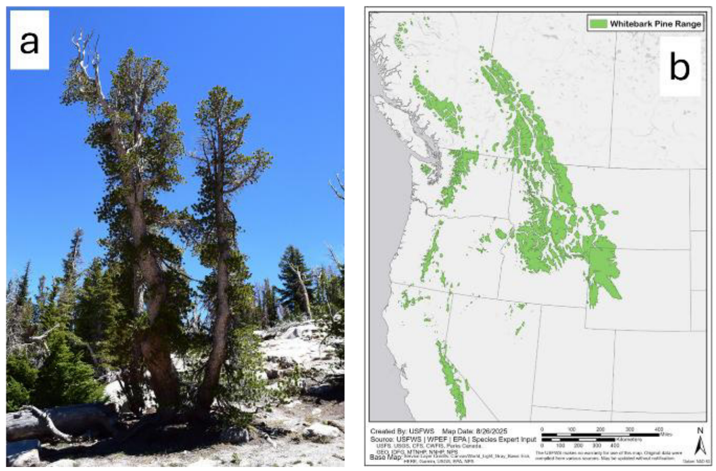

Figure 1. (a) Whitebark pine (*Pinus albicaulis* Engelm.), Sierra Nevada, California. (b) The U.S. and Canadian distribution of whitebark pine. (Photo credit: (a) D.F. Tomback); (b) Map modified from: U.S. Fish and Wildlife Service (2021); range data updated from U.S. Fish and Wildlife Service(2023). https://www.sciencebase.gov/catalog/item/66cf792ad34e98e8a924c06a).

Whitebark pine has two distinct distributional segments: the western portion ranges from about 36 to 55° N latitude, from the southern Sierra Nevada Range north through the coastal ranges of Canada; and the Rocky Mountain portion from about 42 to 54° N latitude, from the Greater Yellowstone Region north through the southern Canadian Rocky Mountains (Figure 1b). Whitebark pine may be a minor to major component of forest communities, which comprise three distinct types with intergradation. Successional communities occur on productive sites in the upper subalpine forest zone, depend on periodic fire for renewal, and are most common across the central and northern Rocky Mountains of the U.S. and adjacent southern Canada (Arno and Hoff 1990). Whitebark pine is an early seral species in these communities, gradually replaced by faster-growing, shade-tolerant species over time, with some individuals persisting late into succession (Campbell and Antos 2003). Whitebark pine in climax communities, which occur on windy sites with poor soils, is self-replacing through seedling establishment; whitebark pine climax communities are the most widely occurring whitebark pine communities across the species' range. Whitebark pine is also a component of treeline communities and assumes a dominant role especially east of the Continental Divide on windy, dry slopes (Arno and Hoff 1990; Tomback et al. 2016a).

The life history of whitebark pine has been shaped by coevolution with its principal seed disperser, Clark's nutcracker (*Nucifraga columbiana*, Family Corvidae) (Lanner 1990; Tomback and Linhart 1990). Seed dispersal by nutcrackers influences the ecology, distribution, and population structure of whitebark pine (Tomback 2001, 2005) and informs seeding methods. In late summer and fall, nutcrackers harvest seed from whitebark pine cones and bury seed caches (typically 1 to 15 seeds per cache) throughout mountain terrain across the elevational gradient from lower treeline to the alpine zone above the upper treeline (Hutchins and Lanner 1982; Tomback 1982, 2001). Seed in suitable sites that are not retrieved by nutcrackers or pilfered by rodents (Order Rodentia) may germinate after one to several years, leading to regeneration (Tomback 1982; Tomback et al. 2001b). Cache site selection by nutcrackers, in conjunction with environmental potential for seed germination and seedling survival and growth, determines where whitebark pine establishes in mountain terrain (Table 1) (Tomback 2001; Lorenz et al. 2011). Seed dispersal in seed clusters often produces multi-genet tree growth forms; and local and long-distance seed dispersal influences population structure at stand, watershed, and regional levels (Tomback and Linhart 1990; Tomback 2005). The distinctive morphology of whitebark pine appears adapted for this interaction: upward-trending branches bearing cone whorls at their tips; cones that remain closed when ripe (indehiscent); large, wingless seeds; and seed morphology and physiology that enable seed to remain viable for years in a soil seed bank (Lanner 1990; Tillman-Sutela et al. 2008; Tomback and Linhart 1990).

Table 1. Characteristics of Clark's nutcracker (*Nucifraga columbiana*) cache sites for whitebark pine (*Pinus albicaulis* Engelm.) seed that potentially impact restoration practice. Information is based on Lorenz et al. (2011), Hutchins and Lanner (1982), and Tomback (1978, 1982, 2001). Note: nutcrackers also place a portion of their caches above ground within trees (e.g., crotch of a fork), but these caches have no regeneration potential (Lorenz et al. 2011; Tomback 1978).

Range of distance seed is moved from the source tree: ~0 m to 33 km
Substrates: mineral soil, volcanic gravel (pumice), conifer needle litter (duff)
Number of seed per cache: $\bar{x}$ = 3–4, range = 1 to 15
Distance between caches: $\bar{x}$ = 67 ± 69 cm (SD), range = 10 to 300 cm
General cache environments: within different forest community types; steep, open slopes; rocky cliffs; talus slopes; rocky rises; meadows; streambanks; lower treeline shrub and tree communities to upper treeline and tundra communities.
Specific cache sites: around tree bases, next to rocks, next to deadfall, next to fallen branches, in sparse vegetation, among tree roots, and in open areas (no feature).

Whitebark pine provides important ecosystem services across its range. Given its broad latitudinal distribution, whitebark pine communities are diverse, varying in tree associates and understory composition (Arno and Hoff 2001; Tomback et al. 2001a; Tomback and Achuff 2010). Whitebark pine stands growing at the highest subalpine elevations and treeline communities redistribute and retain snowpack (Farnes 1990; Tomback et al. 2016a). Its large seeds are an important food for numerous granivorous birds and small mammals as well as bears (*Ursus* spp.); and whitebark pine communities on harsh high elevation sites provide habitat, shelter, nest, and burrow sites for diverse wildlife, including birds of prey (Order Accipitriformes, Falconiformes, and Strigiformes), cervids (including elk (*Cervus canadensis)*, deer (*Odocoileus spp.)*, and moose (*Alces*

alces)), and carnivores (Order Carnivora) (Tomback and Kendall 2001; Tomback et al. 2016a). Tolerance of whitebark pine for harsh environmental conditions and poor soils provides protection (facilitation) for the establishment of other plant species (Callaway 1998; Tomback et al. 2016b); and seed dispersal by nutcrackers leads to comparatively rapid regeneration after fire and other disturbances (Tomback et al. 1993, 2001b). In addition, whitebark pine was an important food resource historically and culturally for several western Native American and First Nation tribes (Moermond 1998; Tomback et al. 2011). Whitebark pine is considered both a keystone and foundation species, given that its communities promote biodiversity and provide locally stable conditions for other plant and animal species (DeGrassi et al. 2019; Ellison et al. 2005; Tomback et al. 2001a).

2 Whitebark pine decline and conservation efforts

The ongoing population losses in whitebark pine are reflected in its global and national conservation status. Whitebark pine is categorized as 'endangered' by the International Union for the Conservation of Nature (Mahalovich and Stritch 2013) and by Canada under the Species at Risk Act (Government of Canada 2012), and it is listed as 'threatened' by the U.S. under the Endangered Species Act (U.S. Fish and Wildlife Service 2022).

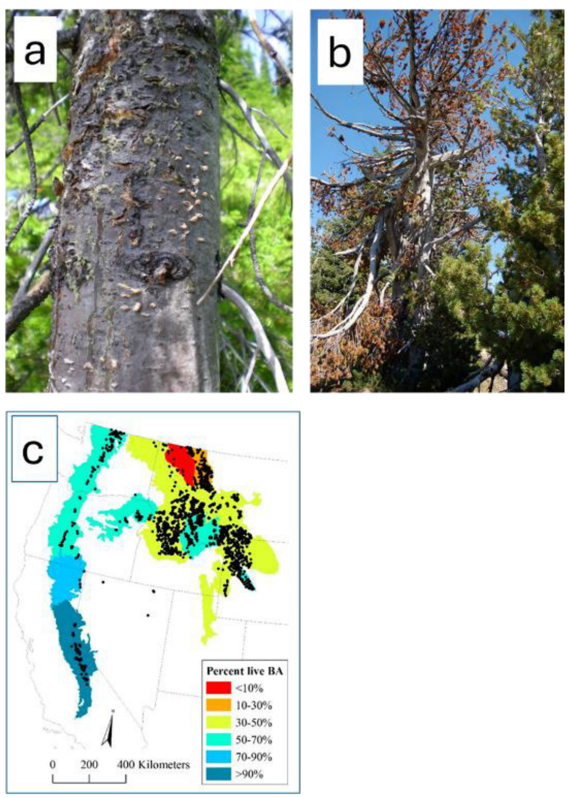

Figure 2. Mortality agents in whitebark pine (*Pinus albicaulis* Engelm.) and extent of decline. (a) Potentially fatal white pine blister rust stem canker in whitebark pine. (b) Whitebark pine killed by mountain pine beetles (*Dendroctonus ponderosae*). (c) From Goeking and Izlar (2019), depicting locations of 1,406 forest inventory plots (black dots) with percentage living basal area of standing whitebark pine trees with diameters ≥ 2.54 cm at breast height within each eco-province, based on plots measured between 2007 and 2016. (Photo credits: (a, b) D.F. Tomback).

The current major threat to whitebark pine is the exotic fungal pathogen *Cronartium ribicola*, which causes the disease white pine blister rust (WPBR) (Figure 2a), that continues to spread throughout the range of whitebark pine (McDonald and Hoff 2001; Tomback and Achuff 2010; U.S. Fish and Wildlife Service 2021). WPBR canopy infections reduce seed production, and stem infections kill trees. Additionally, recent outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have killed mature whitebark pine at an unprecedented scale (Figure 2b; Gibson et al. 2008; Schwandt et al. 2010; Tomback and Achuff 2010). Lastly, historical fire regimes have been altered by fire exclusion and more recently by climate change, which is leading to more frequent, larger, and increasingly severe fires (e.g., Higuera et al. 2021; Keane et al. 2022; Tomback et al. 2022). Climate change is also expected to drive whitebark pine distributional changes (Parks et al. 2025). Compiled U.S. Forest Service Forest Inventory and Analysis data indicated that 51% of standing whitebark pine in the U.S. was dead, with the Northern U.S. Rocky Mountain populations in greatest decline primarily due to WPBR (Figure 2c; Goeking and Izlar 2018). Loss of local and regional seed production decreases the effectiveness of seed dispersal by Clark's nutcracker (Barringer et al. 2012; McKinney and Tomback 2007; McKinney et al. 2009), reducing regeneration rates especially after wildfire (Leirfallom et al. 2015; Stevens-Rumann et al. 2017).

Although the U.S. Fish and Wildlife Service currently is developing the Whitebark Pine Recovery Plan as mandated by the Endangered Species Act, several agencies and inter-agency collaborations previously developed conservation and restoration plans or strategies. A few of these focus on specific restoration treatments or protective actions (e.g., Keane et al. 2012), while others also prioritize a subset of the whitebark pine range for restoration treatments, recognizing the scale of the undertaking even within a region (Jenkins et al. 2022; Tomback and Sprague 2022; Tomback et al. 2022). The primary restoration and conservation approaches and actions used to restore whitebark pine are reviewed in Tomback et al. (2022) and listed in Table 2.

A key restoration strategy is to plant seedlings that are genetically resistant to WPBR (Table 2) (Figure 3), with seeding being piloted as an alternative in areas with limited access and/or land use constraints (Keane et al. 2022; Tomback et al. 2022). Seedling planting is intended to increase the frequency of WPBR-resistant genotypes within populations and compensate for reduced natural regeneration caused by decreasing seed production. Natural resistance to *C. ribicola* exists within whitebark pine populations, and recommended seed sources for seeding and seedling production should be those trees confirmed to have usable genetic resistance to WPBR (Sniezko and Liu 2022). Screening parent trees for genetic resistance to WPBR involves a lengthy (up to 10 years) multi-step process (Figure 4) (Cartwright et al. 2022). Individuals with putative resistance to WPBR must be identified; cones must be collected from trees and processed for storage and screening. Subsequently, seeds are germinated, and seedlings are grown for 2 to 3 years before seedlings are inoculated with WPBR via exposure to high concentrations of *C. ribicola* spores. Trees are then monitored for an additional 3 years before a resistance determination and grade is applied (Sniezko et al. 2023). Elite trees, i.e., those with confirmed resistance to WPBR, then must be protected from other threats including mountain pine beetles (Figure 4).

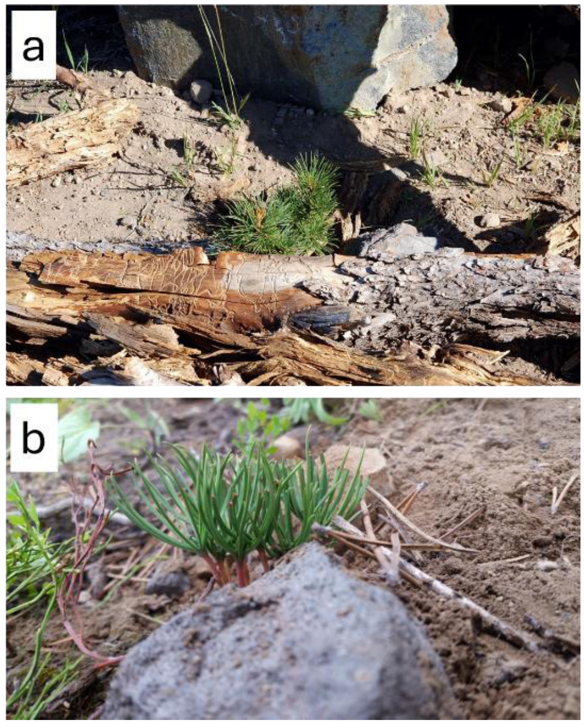

Figure 3. (a) Restoration plantings of whitebark pine (*Pinus albicaulis* Engelm.) seedlings that are from seed sources genetically resistant to white pine blister rust, Crater Lake National Park, Oregon. (b) Natural whitebark pine regeneration in a seedling cluster. Clusters result from the tendency of Clark's nutcrackers (*Nucifraga columbiana*) to bury several seed per cache and to cache near objects such as rocks and fallen trees. (Photo credits: D. F. Tomback).

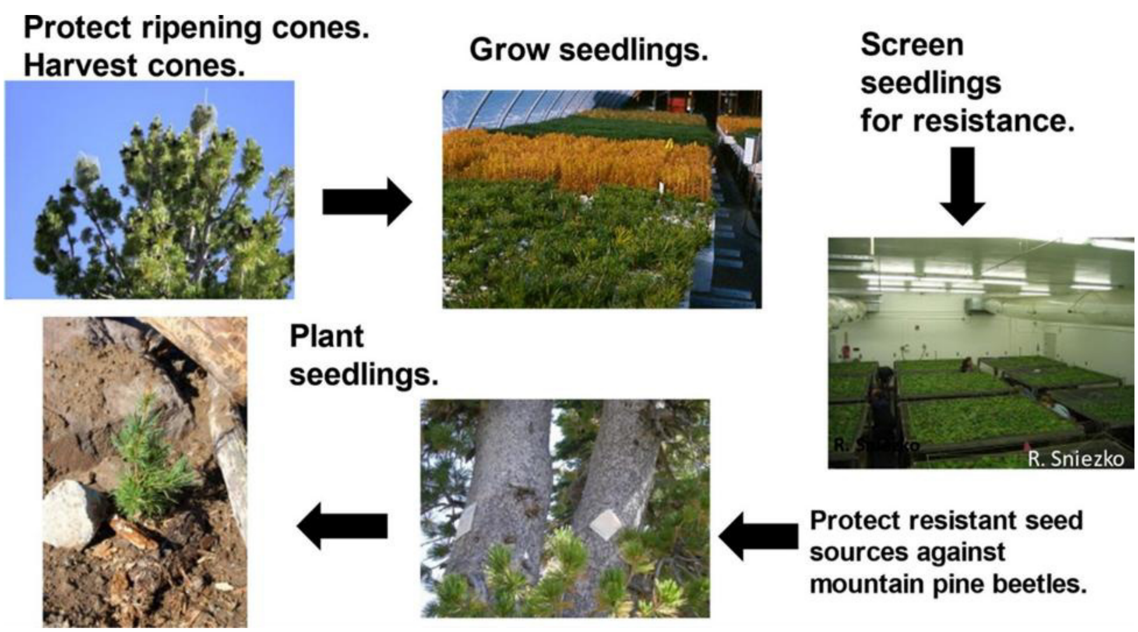

Figure 4. Steps in growing seedlings for screening for genetic resistance to white pine blister rust and for operational planting: Cone protection and harvest, growing seedlings, applying blister rust inoculum, protecting trees with genetic resistance to white pine blister rust from mountain pine beetle (*Dendroctonus ponderosae*) attack, and planting seedlings in protected microsites. (Photo credits: unless otherwise noted, D.F. Tomback; modified from Tomback et al. (2022)).

Table 2. Summary of conservation actions and restoration treatments for whitebark pine (*Pinus albicaulis* Engelm.) from Tomback and Sprague (2022). See Tomback et al. (2022) for guiding principles and a review of currently recommended actions and treatments and Keane et al. (2012, 2022) for basic restoration and conservation principles and restoration approaches under climate change. WPBR = white pine blister rust. MPB = mountain pine beetle (*Dendroctonus ponderosae*).

1. Conserve genetic diversity
● Seed collections for seed archiving.
2. Promote genetic resistance to WPBR
● Identify seed zones across the whitebark pine range.
● Select candidate trees (seed trees and plus—i.e., putatively resistant—trees) for WPBR-resistance screening.
● Screen for genetic resistance to identify trees with useable resistance (elite trees).
● Identify sufficient numbers of resistant trees to conserve genetic diversity.
● Develop seed orchards where appropriate for operational seed production.
3. Grow seedlings to restore populations and build resilience to WPBR and climate change
● Collect cones from elite trees and drought-tolerant trees or those from environments considered similar to future climate change scenarios.
● Optimal goal is to find trees with both WPBR-resistance and drought tolerance.
● Grow seedlings.
● Plant seedlings or sow seed, especially in climate change refugia.
4. Protect trees with known blister rust resistance or high value stands
● Protect trees from attack by MPB.
● Protect trees from fire.
5. Reduce competition in successionally advanced communities
● Apply various silvicultural treatments, depending on conditions and goals.
● Use prescribed fire as a restoration tool.
● Manage wildfires.
6. Implement treatments proactively to build resilience in healthy whitebark pine communities
7. Assess whitebark pine health and stand conditions
● Implement surveys to assess health status and trends.
● Monitor stand health and conditions over time.
8. Develop monitoring plans for restoration treatments and conservation actions
● Integrate monitoring into project planning and management.
● Use monitoring outcomes to adjust treatments for successful restoration and conservation, i.e., adaptive management.

3 Rationale for use of seeding

Although planting WPBR-resistant nursery-grown seedlings will remain the key restoration action for whitebark pine, seeding is being explored as an additional tool for the restoration toolkit. There are two major rationales or justifications for exploring the efficacy of seeding as an alternative to seedling planting and as a restoration practice for whitebark pine. First and foremost, accessibility and/or land use constraints may limit where restoration activities are feasible. Much of the whitebark pine distribution is at high elevations on steep slopes in remote and/or inaccessible terrain where planting becomes infeasible to execute. Additionally, about 29% of the whitebark pine range is within federally designated wilderness (Tomback et al. 2001a; U.S. Fish and Wildlife Service 2021). In the case of the latter, interpretation of the 1964 Wilderness Act by organizations and agencies may restrict the transportation and planting of seedlings in federally designated wilderness (Tomback et al. 2022). Seeding involves less manipulation or 'trammeling,' especially if seed is collected from and sown at the targeted location. With respect to general application, seeding is viewed as a method to restore whitebark pine in inaccessible high elevation terrain, where transporting and planting seedlings becomes challenging if not prohibitive. Given that burned seedbeds are optimal conditions for planting seedlings and seeding, field crews can make use of high elevation burns on steep terrain for sowing seed with far less effort than required for planting. Accessibility and logistical constraints are further expected to become more pointed with a changing climate. Climate change may accelerate whitebark pine decline, progressively shifting suitable habitat to higher elevations (e.g., McKenney et al. 2007; Schrag et al. 2007; Warwell et al. 2007; Hansen et al. 2016; Park et al. 2025). This upward contraction may further isolate potential restoration sites that may act as climate refugia, amplifying the logistical challenges of accessing and restoring sustainable populations. Seeding may facilitate restoration in areas that are priorities for intervention but would otherwise be omitted due to logistical or land-use constraints.

The second rationale for seeding is to reduce costs for restoration projects. For operational seedling production, the cost of nursery facility care plus planting per whitebark pine seedling is more than $3, but this price does not include the expenses of tree climbers, cone caging, cone harvest, transportation, and storage, etc. In contrast, estimated costs for seeding are about $0.20 per seed cache without including costs of harvesting seeds and transportation (Tomback et al. 2022). The trade-off is the efficacy of seedling planting versus seeding. Details are provided below.

4 Development of seeding in whitebark pine ecosystems

The use of seeding to restore whitebark pine communities has a comparatively recent history. Whitebark pine seed is characterized by an underdeveloped embryo, physiological dormancy, and mechanical barriers to germination, requiring specialized treatments and stratification protocols for seedling production in nurseries (McCaughey and Tomback 2001). The primary objectives of the first studies were to examine germination and seedling emergence rates with and without seed treatments, but also the efficacy of treatments to reduce rates of rodent pilferage and different microsite types. Most of the exploratory seeding studies have been implemented in the northwestern United States and the Greater Yellowstone Region.

The objectives of McCaughey (1993), the first documented seeding study, were to compare germination rates of untreated whitebark pine seed between surface-sown seed and buried seed (Table 3). For this study, McCaughey (1993) used a recent clearcut on Palmer Mountain, Gallatin National Forest, Montana, USA. His study deployed 2,880 filled seeds collected nearby, varied shade levels and substrate, and enclosed all plots in wire mesh cloth cages with edges buried to exclude seed predators. Each surface-sown seed was matched by a buried seed within the same subplot. Over three years, significantly more buried seed than surface-sown seed germinated. Seed germination did not differ statistically by shade level or substrate type, although more seedlings emerged from shaded treatments and litter layer treatments. The study indicated that most buried seed that are protected from rodent predation will germinate over time, and that whitebark pine seed often experiences delayed germination—a fact later substantiated for naturally dispersed whitebark pine seed (Tomback et al. 1993, 2001b).

Table 3. Development of seeding as a restoration tool for whitebark pine (*P. albicaulis*). Results of studies that explored the efficacy of various treatments to increase germination rate, reduce losses to rodents, and increase seedling survival are summarized here. See text for additional details. NF = national forest.

Reference	Location	Site preparation	Treatments	Duration	Results
McCaughey (1993)	Palmer Mountain, Gallatin NF, MT, USA.	Clearcut.	1 buried seed; 1 surface seed per treatment. Shade levels (0%, 25%, 50%). Substrate mineral soil, litter. Wire cloth enclosures.	3 years	% Germination: - 56% buried vs. 7% sown on surface. - 60% shaded vs. 47% unshaded. - 60% mineral soil vs. 51% duff.
Schwandt et al. (2007)	Vinegar Hill, Umatilla NF, OR, USA.	Small burn scars from slash pile burning.	Warm stratification. Seed scarification. Scarification and warm stratification. Control. Above 4 treatments in wire cloth enclosures. Rodent repellent Thiram®. [1] Rodent repellent cayenne pepper.[2] No repellent. Logs provided afternoon shade.	9 months (see below)	Only 94 of 700 seeds germinated. Highest germination from both warm stratification treatments. <10% germination for other treatments.
Schwandt et al. (2011)	Vinegar Hill, Umatilla NF, OR, USA. Mt. Bachelor, Deschutes NF, OR, USA. Fairy Lake, Gallatin NF, MT, USA. Thompson Peak, Lolo NF, MT, USA. Ulm Peak, Kootenai NF, MT, USA. Gold Pass, ID, USA Panhandle NF, ID, USA.	Burn scars from natural or prescribed fire.	Warm stratification. Seed scarification. Warm stratification and seed scarification. Control. <u>Vinegar Hill</u>: Above treatments in wire cloth enclosures. Shade provided by logs, snow fences, trees, or snags. <u>Vinegar Hill & Mt. Bachelor only</u>: Rodent repellent Thiram®. [1] Rodent repellent cayenne pepper.[2] No repellent. Mt. Bachelor only Rodent repellent Ropel®.[3] <u>Other sites added</u>: 3 seed caches buried next to planted 2 yr-old seedlings.	Vinegar Hill, 2+ years. Mt. Bachelor, 2+ years. Other study sites (see below)	Vinegar Hill and Mt. Bachelor had the highest germination in the first year with additional germination in the second year but none beyond. Treatments including warm stratification produced the highest seed germination in both study areas (25–72%). Seeds treated with rodent repellents had the lowest germination (8–18%). Preliminary results for the other study areas indicated variable germination, but warm stratification treatments produced the highest percentage germination.
DeMastus (2013)	Fairy Lake[4] and Pioneer Mountain, Custer Gallatin NF,[5] MT, USA. Thompson Peak, Lolo NF, MT, USA. Ulm Peak, Kootenai NF, MT, USA. Gold Pass, ID, USA. Panhandle NF, ID, USA. Toboggan Ridge, Clearwater NF, ID, USA.	Burn scars from natural or prescribed fire (Schwandt et al. 2011). Preparation probably similar for Pioneer Mountain and Toboggan Ridge but not described.	Warm stratification. Seed scarification. Warm stratification and seed scarification. Control. Per treatment block, each treatment both in open and in wire cloth enclosure. 3 or 4 seed caches buried next to planted 2 yr-old seedlings. Soil and below ground temperatures measured in all study areas.	Schwandt et al. (2011) study areas, 3 years. Pioneer Mountain and Toboggan Ridge, 2 years.	The warm stratification had the highest germination rate across study areas (≥41%). Seedling survival rates were study-area specific and varied by treatment. Nursey grown seedlings had higher survival rates than seedlings that emerged during the study. Seedling survival was slightly higher under wire cloth enclosures. Temperature differences did not impact germination rates.

[1]Tetramethylthiuram disulfide [2]*Capsicum annuum* L. [3]Benzyldiethy l[(2,6 xylyl carbamoyl) methyl ammonium sacchari and thymol [4]Fairy Lake study area unsuitable and data not included in final data analysis by Demastus (2013). [5]Custer and Gallatin National Forests merged administratively in 2014.

Schwandt et al. (2007) investigated whether seed treatments (e.g., stratification, scarification) could speed up germination and reduce rodent predation (Table 3). In 2005, they established a trial on Vinegar Hill, Umatilla National Forest, Oregon, USA, using 700 locally sourced whitebark pine seeds. In the study area, small burn scars were selected as sites to install five replicates, with 140 seeds per replicate divided among seven treatments. Three treatments were designed to speed up germination rates, with a fourth control treatment, and all four treatments were enclosed in wire mesh cloth. Two additional treatments tested different substances for efficacy as rodent repellents with a third control treatment (no repellent), and these two rodent repellent treatments and control were exposed to predation. Logs were positioned to provide shade during the afternoon for each replicate. The experimental study area was revisited nine months after installation. Investigators found that the treatments with the highest germination rates were the two with warm stratification. Despite low germination rates overall, the study indicated that treatments potentially could speed up germination.

In 2006, Schwandt et al. (2011) added treatments for seeding, comparing germination success, seedling survival rates, and comparing the survival of seedlings produced from seeding to the survival of nursery-grown seedlings on the same sites, and they also added study areas. They expanded their seeding study beyond Vinegar Hill, Oregon, to Mt. Bachelor, Oregon, and in 2009 to three sites in Montana—Fairy Lake, Thompson Peak, Ulm Peak—and one in Idaho, USA—Gold Pass (Table 3). About 1,000 seeds were obtained near each study area and sown with five replicates of four basic treatments, 20 seeds per treatment. There were additional treatments in some study areas and differences in the setups. Three treatments facilitated seed germination and were compared with an untreated control. The Mt. Bachelor study area also included three rodent repellent treatments and a treatment where small peat pots were used to provide a moist environment for the seed. The 2009 trials also included sowing seed caches adjacent to nursery-grown seedlings in the Montana and Idaho study areas (Table 3). Half the treatments were protected from rodent predation by wire mesh cloth enclosures, and all treatments were shaded (Table 3). The 2005 and 2006 results indicated that most germination occurred in the spring following sowing. Warm stratification treatments were more effective than scarification in facilitating germination. Rodent repellents reduced germination, and the peat pots were destroyed by rodents. At Vinegar Hill, only 20% of seed germinated overall, and most of the cotyledon seedlings were killed by high temperatures after emergence. For Mt. Bachelor, 72% of the caged, warm stratified seed germinated, and seedling survival was greater on cool, northern slopes than on warm aspects. For the 2009 trials, preliminary results indicated that warm stratification of seed produced the highest germination of all treatments or the control, with an average of 47%.

The study objectives for DeMastus (2013) were similar to those of Schwandt et al. (2011) but also included questions about the influence of soil surface and sub-surface temperatures (monitored by sensors and data loggers) (Table 3). His research continued the Schwandt et al. (2007, 2011) studies, using the Fairy Lake, Thompson Peak, Ulm Peak, and Gold Pass study areas noted above; and in 2010, he added the Yellowstone Club ski area in Montana, and Toboggan Ridge in Idaho. The methods did not state whether shade protection for treatment blocks was still provided in these areas, as described in Schwandt et al. (2011). For each study area, DeMastus (2013) collected 800 whitebark pine seeds from local seed sources, using 20 seeds per treatment. Among the blocks, he planted either 34 or 100 two-year-old-seedlings, paired with caches of 3 or 4 seeds, depending on the study area. Data were collected for three years at the sites established in 2009, and for two years at the site established in 2010. Sites differed in maximum and minimum temperatures and extreme weather events, but no association with germination was established. Overall, warm stratification produced the highest average percent germination for most of the sites. Seedling survival was highest across treatments at the Toboggan Ridge site followed by Thompson Peak, with the lowest survival at Ulm Peak, and thus appeared to be site-specific and to vary by treatment. Germination rate was similar between seed with and without wire mesh cloth cover, nursery-grown seedlings had higher survival than seedlings grown from sown seed, seed sown in multi-seed and single-seed caches had similar germination rates overall, and the survival of seedlings from seed sown in clusters vs. single seeds was similar. The slight block dependent advantage of wire mesh cloth enclosures on seedling survival was not considered great enough to justify the work required to deploy the enclosures.

Pansing et al. (2017) approached seeding with a different set of objectives. They aspired to assess, through artificial caches closely simulating nutcracker caches, whether spatial patterns of cache pilferage, germination, and seedling survival might modify the initial spatial pattern of caches made by Clark's nutcrackers and how these modifications may differ between subalpine forest and the alpine treeline ecotone. The studies, although intended to reveal patterns at a local landscape scale, provided important basic information on variation in the success of seeding based on a rigorous experimental design. Pansing et al. (2017) investigated seeding in two locations in the Northern Rocky Mountains: White Calf Mountain, Montana, on the eastern front of Glacier National Park, and Tibbs Butte, Shoshone National Forest, on the Beartooth Plateau within the Greater Yellowstone Ecosystem. Seed was collected from trees within 11 km of these study sites the fall prior to deployments. Seed was sorted to remove low-weight and insect-damaged seeds, and over-wintered at 1.5 °C (cold stratification). In 2012 the researchers created 735 seed caches across both sites, varying cache size from 1 to 7 based on a Poisson distribution of seed cache size and stratifying the placement of caches in two ways—by whitebark pine forest community type (upper subalpine forest or alpine treeline ecotone), as well as among microsites commonly used by Clark's nutcrackers (rock bases, tree bases, or open terrain) (Tomback 1978). Caches were created in the nearest assigned microsite type to randomly generated points; each cache was buried ca. 2.5 cm under substrate. Seed caches were checked in 2013 for rodent pilferage and seed germination and in 2014 for additional seed germination and seedling survival. Ungerminated caches were excavated to document rodent pilferage in 2013, and any remaining seed was carefully reburied. They found that one or more seeds were pilfered from 54% of caches. Of the pilfered caches, 75% lost all seeds and 25% retained one or more seeds. Odds of pilferage were higher at treeline relative to the subalpine, indicating higher risk of seed theft by rodents at treeline. On Tibbs Butte, one or more seeds in 64% of remaining caches germinated in 2013, and one or more additional seeds in 36% of the remaining caches germinated by 2014. In total, one or more seeds germinated in 85% and 46% of the remaining caches by 2014 on Tibbs Butte and White Calf Mtn., respectively.

These results from Pansing et al. (2017) highlight the importance of recognizing delayed germination in whitebark pine, even with cold stratification treatments, when investigating seeding efficacy. At Tibbs Butte, the odds of cache germination, i.e., one or more seeds germinating per cache, were higher at treeline than in the subalpine forest, and odds of germination were higher near rocks than trees. First year cache survival, i.e., one or more seedlings surviving per cache, ranged from 19% in the subalpine forest of White Calf Mtn. to 77% at treeline on Tibbs Butte. The odds of seedling survival were higher at treeline on Tibbs Butte and adjacent to objects (i.e., rocks and trees) relative to open microsites, suggesting that protection at treeline may improve seedling survival outcomes. Similar to the findings of DeMastus (2013), no association between cache germination and cache size was detected.

Pansing and Tomback (2019) continued to follow the seed caches created on Tibbs Butte through 2018 to assess five-year seedling survival. In 2018, they could relocate 162 caches that held one or more seedlings in 2013—68 of the 162 caches contained at least one surviving seedling. Known fate modeling suggested that annual seedling survival rates ranged from 57% in the subalpine forest to 99% at treeline in 2016. Odds of survival were 2.6 times higher at treeline than in the subalpine and varied substantially by year. A model including year and elevation zone, and another including year, elevation zone, and microsite had similar evidence AIC scores suggesting microsites may be influential despite non-significant microsite differences, potentially due to small sample sizes. Year may be a surrogate for annual differences in weather variables such as snowpack, precipitation, or temperature.

Hankin et al. (2023) explored variation in the performance of seedlings produced by seeding in three high elevation five needle white pines (*Pinus* spp. L.), including whitebark pine. Their work aimed to estimate local adaptation and phenotypic plasticity in emerging whitebark pine and other high elevation white pine seedlings, focusing on the impact of weather during emergence and seedling survival. Importantly, it represents the only research published to date on whitebark pine seeding in the southern Sierra Nevada, which comprises a genetically and ecologically distinct population of the species (Richardson et al. 2002; Syring et al. 2016; U.S. Fish and Wildlife Service 2021). Hankin et al. (2023) established a common garden experiment using two whitebark pine seed sources sown in six locations across California and Nevada. Whitebark pine consistently had low emergence rates—between 0.3% and 8.5% in 2020 and 2021 across the six sites, with 0.5% emergence at both sites where whitebark pine is native. The remaining four sites were outside of the whitebark pine range. They found that the establishment environment, specifically summer soil moisture, was the strongest predictor of emergence and abundance of whitebark pine. Further, they identified that the seed source from the drier location, i.e., the site that had higher summer climatic moisture deficit, produced seedlings with a higher root to shoot ratio and lower biomass growth rate.

The studies summarized in Table 3 provide guidance for seeding projects. They indicated that cached whitebark pine seed had much higher germination rates than surface-sown seed and that whitebark pine seed may germinate over a period of several years. Furthermore, warm stratified seed germinated at a higher rate than untreated or scarified seed, rodent repellent reduced seed germination rates, seedling survival varied by study area and by treatment, and that the use of wire mesh cloth enclosures only slightly increased seed germination and seedling survival. The studies by Pansing et al. (2017) and Pansing and Tomback (2019) indicated that seeding that simulated natural caches across a local landscape experience high losses to small mammals, but the remaining caches had >50% cumulative seed germination rates over two years. Seedling survival was surprisingly high at treeline at the Tibbs Butte study area, showing promise for this restoration approach, especially when considering the potential impacts of climate change. The Hankin et al. (2023) paper demonstrated the importance of summer moisture for seed germination in arid environments, which is substantiated by field studies (Tomback et al. 1993, 2001b) and suggests that sites for seeding must be carefully chosen.

5 Seed procurement and preparation

Seed collection for whitebark pine is a costly and labor-intensive process. Most seed is wild-collected, although seed orchards are being developed across the range of the species to facilitate easier collection. Ideally, seed is collected from elite parent trees, although in many locations it is still being collected from trees that are putatively resistant to WPBR or have unknown levels of resistance.

Because whitebark pine seed is sought by wildlife, cone collection protocols differ substantially from other conifer species. In mid spring, trees are surveyed for cone production, and individual trees are identified for collection. In late spring or early summer (June through early July, depending on the geographic region), climbers access trees and place wire mesh cages around developing cones to prevent seed predation by nutcrackers and squirrels. Climbers return to harvest cones once seed has ripened in mid-September through October. Cones are then sent for processing to extract seed and prepare it for storage and later use in restoration plantings.

Research assessing important whitebark pine traits, including WPBR resistance, climate adaptation, drought resistance, and mountain pine beetle resistance is at different stages, but the objective is to inform seed collection and restoration activities. Protocols for harvesting seed and growing seedlings from parent trees with known WPBR resistance are well established and benefit from more than 60 years of research on other white pines (Burr et al. 2001; Schwandt et al. 2010). Efforts are underway to identify key genes that confer WPBR resistance, climate adaptation, and other traits, aided in part by the recently described whitebark pine genome (Figueroa-Corona et al. 2024; Neale et al. 2024; van Mantgem et al. 2023). The highest priority is to identify parent trees with WPBR resistance without the need to screen seedlings. Restoration efforts would be further facilitated by the ability to identify seed sources and to develop protocols to promote climate adaptation, drought resistance, and mountain pine beetle resistance. Climate adaptation focuses restoration efforts on topography and sites where whitebark pine is likely to persist but also can potentially employ assisted migration of better adapted genotypes from areas within the whitebark pine range where current climate is similar to future climate predictions (Tomback et al. 2022). Historically, forest tree seed has always been collected from local sources within designated seed transfer zones with the understanding that local sources are best adapted to local environments. Yet evidence indicates that many tree species are already maladapted to current climates where they are found, suggesting that local seed may not be best, especially as the climate continues to change (Rehfeldt et al. 2012). Current guidance for whitebark pine suggests avoiding movement among seed zones, but this is being reevaluated (Tomback et al. 2022).

The management reality is that whitebark pine seed available for restoration activities is scarce. In general, there are seed shortages for restoration purposes across the western United States, and the lack of work capacity limits the number of seed collections even in years with good cone production (Fargione et al. 2021). Further, loss of existing whitebark pine seed sources from WPBR, mountain pine beetles, and wildfire reduces the number of genotypes we can conserve and use in reforestation activities. Expanding the funding and workforce with skills to collect whitebark pine cones will be integral to the success of future restoration activities including seeding.

6 Seeding protocol

Seeding protocols for whitebark pine share some of the recommendations made for seedling planting, such as avoiding the following conditions: closed canopy, steep slopes, dense understory vegetation, moist swales, and deep friable soils, especially with signs of pocket gopher (Family Geomyidae) disturbance (McCaughey et al. 2009; Tomback et al. 2022). Because whitebark pine historically has regenerated well in post-fire seedbeds, especially in the Northern Rocky Mountains, many managers have targeted comparatively recent burns or burned sites prior to seedling planting to avoid competition and understory plants (Keane et al. 2012; Perkins 2015; Jenkins et al. 2022). Planted seedlings and seeded caches established on southern or western slope aspects are expected to fare better if they are located near natural or artificial shade objects (e.g., McCaughey et al. 2009; Casper et al. 2016). Seeding microsites for most of the studies reviewed above were distributed within the confines of study blocks or plots, but other distribution patterns in relation to natural microsites and certain topography, as well as lower densities, may be more favorable.

Although specific seeding implementation protocols do not exist yet, aside from general site recommendations (Tomback et al. 2022), Pansing et al. (2017) established an experimental, inference-based, and replicable approach that facilitates monitoring of seed pilferage, seed germination, and seedling survival over multiple years. Although sound inference is not necessary to seeding implementation, it is integral to developing sound best management practices and improving outcomes, and it can be integrated with operational seeding to monitor and improve outcomes. Importantly, the methods used simulate Clark's nutcracker caching behavior, under the assumption that this will lead to the highest germination and seedling survival, at least in certain microsites. In addition to selecting the number of seeds per cache from an empirically derived Poisson distribution of seed cache sizes (Tomback 1978; Hutchins and Lanner 1982), burying seed at a similar depth to nutcracker caches (~2.5 cm; Tomback 1978) and creating seed caches at microsites known to be used by nutcrackers (rock, tree, open; Tomback 1978), Pansing et al. (2017) developed a method to precisely relocate caches so they can be excavated to monitor seed pilferage. At each selected cache site, a high precision GPS unit is used to collect and store the location of the cache. To further facilitate cache relocation for monitoring, a square PVC frame (20 cm x 20 cm) and two 8-inch nail spikes are used to mark the location of the cache. Seeds are sown in one vertex of the PVC frame, and one nail spike is hammered into each vertex adjacent to the seed cache (Figure 5). The seed cache is always created upslope of the nail spikes for open microsites and on the northeast side of the object for rock and tree microsites to protect seedlings from excessive sun, high temperatures, and strong winds. A numbered aluminum identification tag is attached to one of the nail spikes to facilitate data collection. When managers return to caches for monitoring, GPS navigation can be used to identify the general vicinity of the cache, and the PVC frame is placed around the nail spikes to identify exactly where the cache was created. Once the location is identified, the cache can be dug up to count the number of seeds remaining in the cache and/or identify seedlings germinated from the cached seed. This approach to locating seedlings has shown to be effective over as many as 5 years (Pansing and Tomback 2019). In the last few years, this suite of methods has been adopted by various federal agencies for experimental trials examining the utility of seeding as a restoration tool.

Figure 5. Monitoring framework as developed by Pansing et al. (2017). The PVC frame is placed such that two nail spikes are visible in two opposing vertices of the frame. The seed cache is located in the vertex nearest the tree. Between this marking process and GPS coordinates, it is possible to track individual seed caches and even dig up seeds to assess cache pilferage. (Photo credit: E.R. Pansing).

For operational application, seeding configurations and selection criteria for seeding may be developed to better align with management goals and desired future conditions. For example, there may be an established tree density target. However, there may be trade-offs between the density of seeded caches and the probability of attracting rodents to the planting projects, and site weather conditions or water balance characteristics may impact demographic processes. A thorough understanding of the impacts of uncontrollable variables on site selection and planning will be necessary to ensure long-term success. Even in operational applications, monitoring will be key to developing and improving best practices.

Currently, information about soil types that best support seeding is limited; soil types vary considerably across the range of whitebark pine, a product of regional and local geological history as well as local ecological processes (Arno and Hoff 1990). Research is just beginning to examine the impact of water balance variables on planted seedlings, sown seed, and whitebark pine recruitment (e.g., Laufenberg et al. 2020; Hankin et al. 2023), focusing on factors such as evapotranspiration (AET) thresholds and soil moisture, and their association with growth rates and root to shoot ratios. For example, Laufenberg et al. (2020) found that whitebark pine seedling growth rates were highest when cumulative growing season AET was greater than 350 mm. Research into water balance variables associated with seeding may provide key recommendations for restoration protocols that minimize water deficit. Water balance studies may help managers understand the requirements of whitebark pine early growth stages, and especially the impact of water balance on whitebark pine seed germination and seedling establishment.

7 Monitoring

Given that seeding as a restoration tool for whitebark pine is still very much under development, monitoring outcomes becomes an essential component of seeding projects (Tomback et al. 2022). The geographic variation in climate and biophysical conditions across the whitebark pine range will likely require that seeding protocols vary at scales from local to regional. As projects are developed and implemented, managers should include monitoring strategies during the planning phase so they may assess project outcomes to improve future protocols. Projects can also be developed with a learning component through stratification of seeding efforts by microsite, slope aspect, elevation, and habitat characteristic, such as burn severity or canopy closure. The major monitoring challenge for seeding is devising some way to mark cache sites that is compatible with agency restrictions and land use types.

There are guiding principles for ecological restoration monitoring that are relevant for achieving 'active adaptive management' in seeding applications (Hutto and Belote 2013; Larson et al. 2013; Gann et al. 2019). These are used in a broader sense for plant ecological restoration but can be applied to seeding specifically. For example, *implementation monitoring* can be used to assess how seeding was performed for the project and could include variables such as weather, seed density, number of seeds per 'cache,' seeding depth, and microsite types. A monitoring strategy should capture the variation in implementation with sufficient sample sizes so that comparisons within each variable are possible. *Efficacy monitoring* in principle examines whether project restoration objectives were met, or some progress can be documented towards objectives, such as density of seedlings produced and seedling survival rates after a designated timeframe. Monitoring considerations might include when to sample, such as after years 1, 3, and 5, how much of the project to sample, and how to distribute monitoring across the project (Tomback et al. 2022).

Because whitebark pine seeding is still under development as a restoration tool, implementation and efficacy monitoring will enable us to better understand how to improve outcomes and reduce outcome variation, ensure operational efficiency, and confirm that restoration objectives are being met. Monitoring seeding presents its own unique challenge. Whitebark pine seed must be buried to maximize germination, and returning to the exact location of a seed cache is difficult. This challenge is even greater when seed caches must be dug up to assess cache pilferage rates. Marking caches is necessary to ensure that information on the cache location is sufficiently accurate that pilferage and lack of germination are not confounded, and naturally regenerating seedlings are not confused with seedlings generated from seeding (see Figure 3b). Confounding pilferage and germination failure can prohibit identification and testing of solutions specific to each recruitment phase. Although monitoring methods have been developed, some key aspects of seeding life history, such as number of years required for successful establishment, which informs optimal monitoring timelines and frequencies, remain to be determined.

8 Challenges to operationalizing seeding

Although seeding holds promise for whitebark pine restoration, substantial barriers remain to effective operationalization. Solutions to these challenges are likely to vary in utility depending on geographic context, land-use designation, and implementation phase.

Seed pilferage by rodents is one of the most significant barriers to implementation and social acceptance. Various mitigation techniques, such as wire mesh cloth cages, cayenne pepper, and the fungicide Thiram, as discussed above (Schwandt et al. 2006; Schwandt et al. 2011; DeMastus 2013), along with emerging technologies like seed crowns and nursery pods (e.g., W. Scott Laseter, personal communication, Marc Swackhamer personal communication), have shown promise but also mixed results. However, protective installations including wire mesh cloth and seed crowns are often prohibited in proposed and designated Wilderness Areas; they add substantial labor and costs for both installation and removal; and they require extra site trips for removal. Pilferage is a critical concern, because whitebark pine seed collection is costly, time-intensive, and laborious (Tomback and Sprague 2022), making "wasted" seed a significant resource loss. However, comparative studies have yet to assess seed efficiency between seeding and greenhouse-grown seedlings. DeMastus (2013) found higher survival rates of outplanted seedlings compared to combined seed germination and seedling survival rates for directly sown seeds. However, comparisons of survival of outplanted seedlings to germination and seedling survival of sown seed overlook nursery processes that obscure seed use efficiency. For example, nursery germination rates for whitebark pine range from 28% to 90%, and personnel will often place two seeds in each seedling container to optimize space in greenhouse settings (Olsen et al. 2016). Assumptions that seeding wastes more seed than outplanted seedlings have not been assessed and require examination.

Another barrier is the uncertainty in outcomes associated with seeding. Whitebark pine seed collections can be a limiting factor in the initiation of operational seedling planting or seeding projects. The priority is to grow seedlings or sow seed that have some genetic resistance to WPBR (Tomback et al. 2022). Given that the overall success of seeding projects currently is highly variable, there is a reluctance to invest seed from resistant seed sources, time, and personnel costs. On the other hand, seeding is one of the only restoration tools that is permitted for use in Wilderness Areas, which comprise a high proportion of some federal lands, such as National Park units and many National Forests of the U.S. Forest Service and are predicted to comprise a relatively higher proportion of whitebark pine habitat less impacted by climate change in the foreseeable future (Parks et al. 2025). As we work to better understand and reduce the variation associated with seeding outcomes, managers need to evaluate the tradeoffs between uncertain outcomes and the consequences of not restoring priority areas.

Monitoring seeding outcomes presents additional logistical challenges, as consistent year-to-year measurements necessitate marked installations to relocate caches and their seedlings (e.g., Figure 5). Existing studies rely on specific markers to facilitate re-measurement and data consistency (e.g., Schwandt et al. 2007; Pansing et al. 2017), yet use of these markers is often restricted in Wilderness Areas. Furthermore, if seeding is being implemented by agencies, more reporting of outcomes from seeding trials would benefit managers across agencies, underscoring an urgent need for broader dissemination of trial results. Published findings will be critical for refining protocols and guidance for land managers, ultimately bolstering the success of seeding operations.

Finally, current guidance on seeding lacks specificity regarding optimal techniques and locations, primarily because recommendations have been constrained by geographically limited trials with small sample sizes. Modifications to standard seedling planting densities, for example, may be required to align with the unique needs of seeding and to mitigate pilferage rates. Preliminary evidence suggests that microsite selection may significantly influence seeding outcomes (e.g., Pansing et al. 2017), yet further research is needed to offer land managers informed, location-specific recommendations.

9 The road ahead

Better understanding of the factors affecting variation in seeding outcomes and how managers can increase seeding success may be essential before we see general adoption of this method as a restoration tool for whitebark pine. Although variation in outcomes from site-specific differences, including soils, regional and local weather, and climate change impacts, are expected, methodical, controlled research spanning multiple sites, regions, and years will be required to refine recommendations to land managers. As additional information on the impacts of site-specific characteristics on whitebark pine seeding success becomes available, we need to encourage managers to disseminate the results.

Despite ongoing challenges, interest in the use of seeding for whitebark pine restoration is expanding across federal lands in the western U.S. While there is still work to be done to standardize outcomes and develop protocols adaptable to diverse geographies and jurisdictions, seeding is emerging as a valuable tool in the whitebark pine restoration toolkit. Land managers increasingly recognize its potential, particularly in hard-to-access areas where traditional seedling planting is impractical or restricted. As more data from seeding trials become available—alongside best management practices and a boost in seed collection efforts across the West—seeding is poised to become a more widely adopted method for restoring whitebark pine in remote high-priority locations that would otherwise remain unrestored. Inaction could potentially result in local extirpation of this important forest resource.

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11 References

Arno SF, Hoff RJ (1990) *Pinus albicaulis* Engelm. Whitebark pine. In: Burns RP, Honkala BH (eds), Silvics of North America, Volume 1, Conifers. Agriculture Handbook 654, USDA Forest Service, Washington, DC, USA, pp 268–279.

Barringer L, Tomback DF, Wunder MB, McKinney ST (2012) Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's Nutcracker. PLOS ONE 7:1–11, e37663. https://doi.org/10.1371/journal.pone.0037663

Burr KE, Eramian A, Eggleston K (2001) Growing whitebark pine seedlings for restoration. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 325–345.

Callaway RM (1998) Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos 2:561–573. https://doi.org/10.2307/3546376

Campbell EM, Antos JA (2003) Postfire succession in *Pinus albicaulis – Abies lasiocarpa* forests of southern British Columbia. Can J Bot 82:383–397. https://doi.org/10.1139/b03-040

Cartwright C, Sniezko RA, Reid I (2022) Whitebark pine genecology trials in British Columbia: age 5 results. For Ecol Manag 521:120419 https://doi.org/10.1016/j.foreco.2022.120419

Casper AMA, Jacobi WR, Schoettle AW, Burns KS (2016) Restoration planting options for limber pine (*Pinus flexilis* James) in the Southern Rocky Mountains. J Torrey Bot Soc 143:21–37. https://doi.org/10.3159/TORREY-D-14-00085

COSEWIC (2010) COSEWIC assessment and status report on the Whitebark Pine *Pinus albicaulis* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, CA.

Degrassi AL, Brantley S, Levine CR, Mohan J, Record S, Tomback DF, Ellison AM (2019) Loss of foundation species revisited: conceptual framework with lessons learned from eastern hemlock and whitebark pine. Ecosphere 10(11): e02917. https://doi.org/10.1002/ecs2.2917

DeMastus CR (2013) Effective methods of regenerating whitebark pine (*Pinus albicaulis*) through direct seeding. MSc Thesis, Montana State University, Bozeman, Montana, USA. 114 pp.

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Farnes PE (1990) SNOTEL and snow course data: describing the hydrology of whitebark pine ecosystems. In: Schmidt WC, McDonald KJ (comps) Proceedings – Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, General Technical Report INT-270, Ogden, UT, USA, pp 302–304.

Figueroa-Corona L, Baesen K, Bhattarai A, Kegley A, Sniezko RA, Wegrzyn J, De La Torre AR (2024) Transcriptional profiling of early defense response to white pine blister rust infection in *Pinus albicaulis* (Whitebark Pine). Genes 15(5):602. https://doi.org/10.3390/genes15050602

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, Hallett JG, Eisenberg C, Guariguata MR, Liu J, Hua F (2019) International principles and standards for the practice of ecological restoration. Restor Ecol 27:S1–S46. https://doi.org/10.1111/rec.13035

Gibson K, Skov K, Kegley S, Jorgensen C, Smith S, Witcosky J (2008) Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. USDA Forest Service, Forest Health Protection R1-08-020, Missoula, MT, USA.

Goeking SA, Izlar DK (2018) *Pinus albicaulis* Engelm. (Whitebark Pine) in mixed-species stands throughout its U.S. range: broad-scale indicators of extent and recent decline. Forests 9:131. https://doi.org/10.3390/f9030131

Government of Canada (2012) Order amending Schedule 1 to the Species at Risk Act. Canada Gazette Part II 146(14): SOR/2012–113.

Hankin LE, Leger EA, Bisbing SM (2023) Reforestation of high elevation pines: Direct seeding success depends on seed source and sowing environment. Ecol Appl 33(6):e2897. https://doi.org/10.1002/eap.2897

Higuera PE, Shuman BN, Wolf KD (2021) Rocky Mountain subalpine forests now burning more than any time in recent millennia. PNAS 118(25):e2103135118. https://doi.org/10.1073/pnas.2103135118

Hutchins HE, Lanner RM (1982) The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–210. https://doi.org/10.1007/BF00384487

Hutto RL, Belote R (2013) Distinguishing four types of monitoring based on the questions they address. For Ecol Manag 289:183–189. https://doi.org/10.1016/j.foreco.2012.10.005

Jenkins MB, Schoettle AW, Wright JW, Anderson KA, Fortier J, Hoang L, Incashola Jr T, Keane RE, Krakowski J, LaFleur D, Mellmann-Brown S, Meyer ED, Pete S, Renwick K, Sissons RA (2022) Restoring a forest keystone species: A plan for the restoration of whitebark pine (*Pinus albicaulis* Engelm.) in the Crown of the Continent Ecosystem. For Ecol Manag 522:120282. https://doi.org/10.1016/j.foreco.2022.120282

Keane RE, Tomback DF, Aubry CA, Bower AD, Campbell EM, Cripps CL, Jenkins MB, Mahalovich MF, Manning M, McKinney ST, Murray MP, Perkins DL, Reinhart DP, Ryan C, Schoettle AW, Smith CM (2012) A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). USDA Forest

Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-279, Fort Collins, CO, USA.

Keane RE, Schoettle AW, Tomback DF (2022) Effective practices for managing resilient high elevation five-needle white pine forests in western North America at multiple scales under changing climates. For Ecol Manag 505:119939. https://doi.org/10.1016/j.foreco.2021.119939

Lanner RM (1990) Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt WC, McDonald KJ (comps) Proceedings – Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, General Technical Report INT-270, Ogden, UT, USA, pp 14–24.

Larson AJ, Belote RT, Williamson MA, Aplet GH (2013) Making monitoring count: Project design for active adaptive management. J For 111:348–356. https://doi.org/10.5849/jof.13-021

Laufenberg D, Thoma D, Hansen A, Hu J (2020) Biophysical gradients and performance of whitebark pine plantings in the Greater Yellowstone ecosystem. Forests 11:119. https://doi.org/10.3390/f11010119

Leirfallom SB, Keane RE, Tomback DF, Dubrowski S (2015) The effects of seed source health on whitebark pine (*Pinus albicaulis*) regeneration density after wildfire. Can J For Res 45:1597–1606. https://doi.org/10.1139/cjfr-2015-0043

Lorenz TJ, Sullivan KA, Bakian AV, Aubry CA (2011) Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). The Auk 128:237–247. https://doi.org/10.1525/auk.2011.10101

Mahalovich M, Stritch L (2013) *Pinus albicaulis*. The IUCN Red List of Threatened Species: https://www.iucnredlist.org/species/39049/2885918 (last accessed 20 April 2021)

McCaughey WW (1993) Delayed germination and seedling emergence of *Pinus albicaulis* in a high elevation clearcut in Montana, USA. In: Edwards DGW (comp) Dormancy and barriers to germination. Proceedings of an international symposium of the International Union of Forestry Research Organizations (IUFRO) Project Group P2.04-00. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia, Canada, pp 67–72.

McCaughey WW, Schmidt WC (2001) Chapter 2 – Taxonomy, distribution, and history. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 29–40.

McCaughey WW, Tomback DF (2001) Chapter 6 – The natural regeneration process. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 105–120.

McCaughey WW, Scott GL, Izlar K (2009) Whitebark pine planting guidelines. West J Appl For 24:163–166. https://doi.org/10.1093/wjaf/24.3.163

McDonald GI, Hoff RJ (2001) Chapter 10 – Blister rust: an introduced plague. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 193–220.

McKinney ST, Tomback DF (2007) The influence of white pine blister rust on seed dispersal in whitebark pine. Can J For Res 37:1044–1057. https://doi.org/10.1139/X06-305

McKinney ST, Fiedler CE, Tomback DF (2009) Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecol Appl 19:597–607. https://doi.org/10.1890/08-0151.1

Moerman DE (1998) Native American ethnobotany. Timber Press, Portland, Oregon, USA.

Neale DB, Zimin AV, Meltzer A, Bhattarai A, Amee M, Corona LF, Allen BJ, Puiu D, Wright J, De La Torre AR, McGuire PE, Timp W, Salzberg SL, Wegrzyn JL (2024) A genome sequence for the threatened whitebark pine. G3: Genes, Genomes, Genetics 14(5), jkae061. https://doi.org/10.1093/g3journal/jkae061

Ogilvie RT (1990) Distribution and ecology of whitebark pine in western Canada. In: Schmidt WC, McDonald KJ (comps) Proceedings – Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, General Technical Report INT-270, Ogden, UT, USA, pp 54–60.

Olsen EC, Park J, Robertson N, Eramian A (2016) Current practices for growing whitebark pine seedlings at the U.S. Department of Agriculture, Forest Service, Coeur d'Alene Nursery. Tree Planters Notes 59(1):64–68.

Pansing ER, Tomback DF (2019) Survival of whitebark pine seedlings grown from direct seeding: Implications for regeneration and restoration under climate change. Forests 10(8):677. https://doi.org/10.3390/f10080677

Pansing ER, Tomback DF, Wunder MB, French JP, Wagner AC (2017) Microsite and elevation zone effects on seed pilferage, germination, and seedling survival during early whitebark pine recruitment. Ecol Evol 7:9027–9040. https://doi.org/10.1002/ece3.3421

Parks SA, Hefty KL, Rushing JF, Goeking SA, Tomback DF, Hood SM, Toney JC, Harrell DL, Lindstrom J, Naficy CE, Slaton MR, Soderquist BS, Taylor EJ (2025) Whitebark pine in the U.S. projected to experience an 80% reduction in climatically suitable area by mid-21st century. Environ Res Lett 20:104012. https://doi.org/10.1088/1748-9326/adfcef

Perkins JL (2015) Fire enhances whitebark pine seedling establishment, survival, and growth. Fire Ecol 11:84–99. https://doi.org/10.4996/fireecology.1102084

Rehfeldt GE, Crookston NL, Moc C, Saénz-Romero S, Campbell EM (2012) North American vegetation model for land-use planning in a changing climate: a solution to large classification problems. Ecol Appl 22(1):119–141. https://doi.org/10.1890/11-0495.1

Richardson BA, Brunsfeld SJ, Klopfenstein B (2002) DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Mol Ecol 11:215–227. https://doi.org/10.1046/j.1365-294X.2002.01435.x

Schwandt JW, Tomback DF, Keane RE, McCaughey WW, Kearns HSJ (2007) First year results of a whitebark pine seed planting trial near Baker City, OR. In: Goheen EM, Sniezko RA (tech coords) Proceedings of the conference – Whitebark pine: A Pacific Coast perspective. USDA Forest Service, Pacific Northwest Region, R6-NR-FHP-2007-01, Portland, OR, USA, pp 132–138.

Schwandt JW, Lockman IB, Kliejunas JT, Muir JA (2010) Current health issues and management strategies for white pines in the western United States and Canada. For Pathol 40:226–250. https://doi.org/10.1111/j.1439-0329.2010.00656.x

Schwandt JW, Chadwick K, Kearns HSJ (2011) Whitebark pine direct seeding trials in the Pacific Northwest. In: Keane RE, Tomback DF, Murray MP, Smith CM (eds) The future of high-elevation, five-needle white pines in western North America: Proceedings of the High Five Symposium. USDA Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-63, Fort Collins, CO, pp 357–361.

Sniezko RA, Liu J-J (2022) Genetic resistance to white pine blister rust, restoration options, and potential use of biotechnology. For Ecol Manag 520:120168. https://doi.org/10.1016/j.foreco.2022.120168

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT (2017) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243-252. https://doi.org/10.1111/ele.12889

Syring JV, Tennessen JA, Jennings TN, Wegrzyn J, Scelfo-Dalbey C, Cronn R (2016) Targeted capture sequencing in whitebark pine reveals range-wide demographic and adaptive patterns despite challenges of a large, repetitive genome. Front Plant Sci 7:484. https://doi.org/10.3389/fpls.2016.00484

Tillman-Sutela E, Kauppi A, Karppinen K, Tomback DF (2008) Variant maturity in seed structures of *Pinus albicaulis* (Engelm.) and *Pinus sibirica* (Du Tour): key to a soil seed bank, unusual among conifers? Trees 22:225–236. https://doi.org/10.1007/s00468-007-0179-2

Tomback DF (1978) Foraging strategies of Clark's nutcracker. Living Bird 16:123-161.

Tomback DF (1982) Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. J Anim Ecol 51:451–467. https://doi.org/10.2307/3976

Tomback DF, Linhart YB (1990) The evolution of bird-dispersed pines. Evol Ecol 4:185–219. https://doi.org/10.1007/BF02214330

Tomback DF, Sund SK, Hoffmann LA (1993) Post-fire regeneration of *Pinus albicaulis*: Height-age relationships, age structure, and microsite characteristics. Can J For Res 23:113–119. https://doi.org/10.1139/x93-018

Tomback DF (2001) Chapter 5 – Clark's nutcracker: Agent of regeneration. In: Tomback DF, Arno SF, Keane, RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 89–104.

Tomback DF, Arno SF, Keane RE (2001a) Chapter 1 – The compelling case for management intervention. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 3–25.

Tomback DF, Anderies AJ, Carsey KS, Powell ML, Mellmann-Brown S (2001b) Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology 82:2587–2600. https://doi.org/10.1890/0012-9658(2001)082[2587:DSGIWP]2.0.CO;2

Tomback DF, Kendall KC (2001) Chapter 12 – Biodiversity losses: The downward spiral. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA, pp 243–262.

Tomback DF (2005) Chapter 7 – The impact of seed dispersal by Clark's nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. In: Broll G, Keplin B (eds) Mountain ecosystems: studies in treeline ecology. Springer, Berlin, Germany, pp 181–201.

Tomback DF, Achuff P (2010) Blister rust and western forest biodiversity: ecology, values, and outlook for white pines. Forest Pathol 40:186–225. https://doi.org/10.1111/j.1439-0329.2010.00655.x

Tomback DF, Achuff P, Schoettle AW, Schwandt JW, Mastrogiuseppe RJ (2011) The magnificent high-elevation five-needle white pines: ecological roles and future outlook. In: Keane RE, Tomback DF, Murray MP, Smith CM (eds) The future of high-elevation, five-needle white pines in western North America: Proceedings of the High Five Symposium. USDA Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-63, Fort Collins, CO, USA, pp 2–28.

Tomback DF, Resler LM, Keane RE, Pansing ER, Andrade AJ, Wagner AC (2016a) Community structure, biodiversity, and ecosystem services in treeline whitebark pine communities: potential impacts from a non-native pathogen. Forests 7:21. https://doi.org/10.3390/f7010021

Tomback DF, Blakeslee SC, Wagner AC, Wunder MB, Resler LM, Pyatt JC, Diaz S (2016b) Whitebark pine facilitation at treeline: Potential interactions for disruption by an invasive pathogen. Ecol Evolution 6(15):5144-5157. https://doi.org/10.1002/ece3.2198

Tomback DF, Sprague E (2022) The National Whitebark Pine Restoration Plan: restoration model for the high elevation five-needle white pines. For Ecol Manag 521: 120204. https://doi.org/10.1016/j.foreco.2022.120204

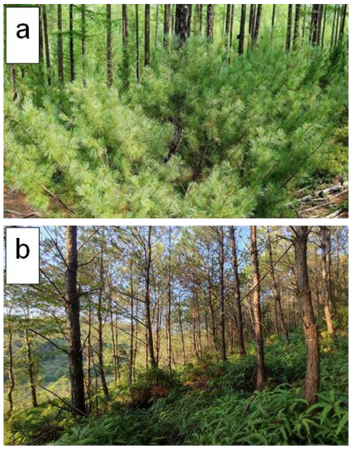
Tomback DF, Keane RE, Schoettle AW, Sniezko RA, Jenkins MB, Nelson CR, Bower AD, DeMastus CR, Guiberson E, Krakowski J, Murray MP, Pansing ER, Shamhart J (2022) Tamm Review: Current and recommended management practices for the restoration of whitebark pine (*Pinus albicaulis* Engelm.), an imperiled high-elevation western North American forest tree. For Ecol Manag 522:119929. https://doi.org/10.1016/j.foreco.2021.119929

US Fish and Wildlife Service (2021) Species Status Assessment report for whitebark pine, *Pinus albicaulis*. Wyoming Ecological Service Field Office. December 2021, Version 1.3.

US Fish and Wildlife Service (2022) Endangered and threatened wildlife and plants; Threatened species status with section 4(d) rule for whitebark pine (*Pinus albicaulis*). Federal Register 87, No. 240:76882–76917.

US Fish and Wildlife Service (2023) Species Range Project. Whitebark Pine (*Pinus albicaulis*) SDM. Data available at: https://www.sciencebase.gov/catalog/item/66cf792ad34e98e8a924c06a

van Mantgem PJ, Milano ER, Dudney J, Nesmith JCB, Vandergast AG, Zald HSJ (2023) Growth, drought response, and climate-associated genomic structure in whitebark pine in the Sierra Nevada of California. Ecol Evol 13:e10072. https://doi.org/10.1002/ece3.10072



Pinus massoniana seeding practices for forest restoration in China

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Abstract

Previous afforestation effort, much of which was accomplished with aerial seeding, restored *Pinus massoniana* Lamb. forests across more than 4 million ha of barren lands and difficult mountainous terrain in Ganzhou, Jiangxi Province, China. This manuscript provides a review of literature reporting the factors that led to forest and site degradation, conventional practices and techniques used to widely establish forest cover of *P. massoniana*, and post-sowing and plantation management practices used to encourage development and growth of restored *P. massoniana* forests. Factors known to impede successful seeding of *P. massoniana* include poor seed quality, harsh soil and site conditions such as soil erosion and droughty soil, unpredictable and extreme weather or climatic events including drought, frost, or excessive rainfall, and insufficient site preparation or plantation maintenance. Procuring high-quality seed, conducting thorough site assessments, and implementing practices that effectively mitigate factors that limit seed germination, seedling establishment, and tree growth are key to successful *P. massoniana* seeding.

Keywords

Mason’s pine, direct seeding, aerial seeding

Contents

1 The region

Ganzhou, the largest administrative region in Jiangxi Province, China, has a warm and humid subtropical climate, creating favorable conditions for the growth of trees and forests (Figure 1). Historically, it was an area very rich in forest vegetation, but due to wars and over-harvesting, its native forest has been seriously degraded and reduced. By the early 1980s, about 6.8 million ha of forests suffered extensive environmental degradation and severe soil erosion. To effectively improve the ecology and environment of the region, Ganzhou carried out the Greening Gannan Action from 1985 to 1994. In barren lands and forestland of difficult terrain conditions, more than 4 million ha of *Pinus massoniana* Lamb. forests were created through afforestation with aerial seeding and planting seedlings (Pan et al. 2019). Forest cover in the region has increased to 76.2%, which has played an important role in improving local ecological and environmental conditions, effectively curbing land degradation, and reducing soil erosion.

1.1 Physiographic region and climate

Ganzhou is located between 24° 29′ and 27° 09′ N latitudes and 113° 54′ and 116° 38′ E longitudes. With a latitudinal distance of 295 kilometers and a longitudinal distance of 219 km, the region has a land area of 39,400 sq km, accounting for 23.6 % of the total land area of Jiangxi Province (Figure 1).

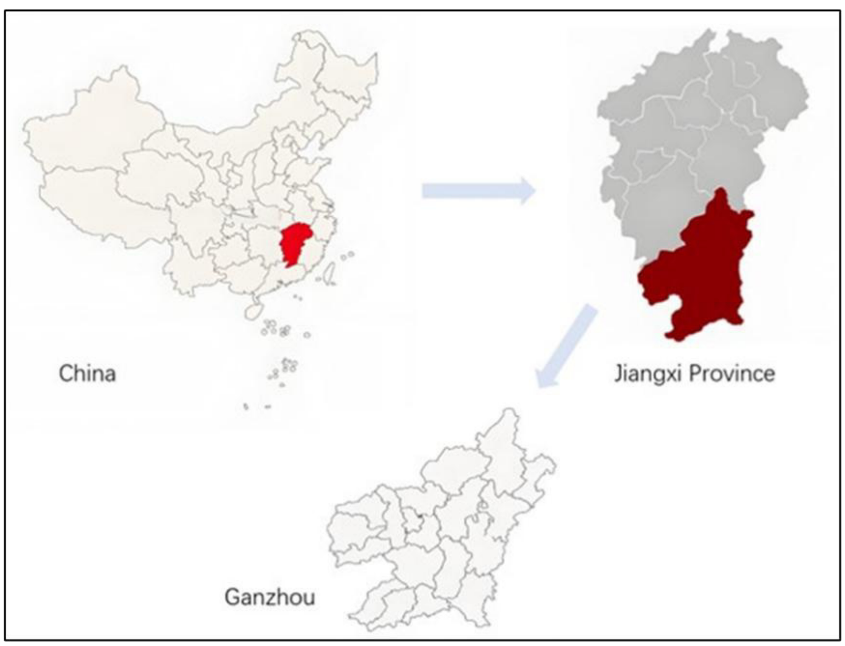

Figure 1. The location of Ganzhou in the Jiangxi Province of China.

Ganzhou is located on the northern edge of the southern subtropical zone and the southern edge of the central subtropical zone. The subtropical hilly and mountainous humid monsoon climate prevails, with precipitation concentrated in spring and summer, and the region experiencing four distinct seasons. The average annual temperature is 18.9 ° C, the average daily temperature in the warmest month is 38.6 °C, the average daily temperature in the coolest month is -7.9 °C, the average annual rainfall is 1526 to 1700 mm, and the average annual frost-free period is 282 to 293 days. According to IPCC (2023), average global temperatures are likely to rise by more than 1.5 °C above pre-industrial levels by 2050, likely resulting in an increase in the frequency and magnitude of extreme events, such as extremely high temperatures and heavy rainfall events.

A variety of soils occur in Ganzhou. Primary soil parent materials are granite, purple shale, slate, sandstone, limestone, gneiss, and Quaternary red clay. Based on the USDA classification system (Soil Survey Staff 2022), the main soils in the region are Ultisols, which are derived from weathered red sandstone and mudstone.

1.2 The forest

P. massoniana (Masson's pine, horsetail pine) is the primary overstory species of forests created through afforestation in Ganzhou. It can tolerate infertile soil and drought and grows on clay, sand, gravel ridges and slopes, and in exposed crevices in rocks. The species grows best in acidic to slightly acidic soil (pH 4.5–6.5). It grows poorly on waterlogged sites and is intolerant of salts and alkalinity in calcareous soils.

The understory vegetation of *P. massoniana* forests is relatively rich with understory shrubs including *Glochidion puberum* (L.) Hutch*., Loropetalum chinense* (R.Br.) Oliv., *Lespedeza bicolor* Turcz., *Rhododendron simsii* Planch., *Eurya japonica* Thunberg, *Phyllanthus urinaria* L., *Symplocos tanakana* Nakai, and *Gardenia jasminoides* J. Ellis. Other understory vegetation mainly includes *Dicranopteris dichotoma* (Thunb.) Bernh., *Imperata cylindrica* (L.) P. Beauv., *Miscanthus floridulus* (Labill.) Warb. ex K. Schum. & Lauterb., *Agropyron cristatum* (L.) Gaertn., *Ischaemum ciliare* Retz., *Paspalum orbiculare* Forst., *Poa annua* L., *Eriachne pallescens* R. Br., *Carex parva* Nees, and *Pteridium aquilinum* (L.) Kuhn.

The region is dominated by young forests, mostly ranging from 16 to 33 years old. The average diameter at breast height (DBH) ranges from 7.6 cm to 19.0 cm, the average dominant height ranges from 7.4 m to 18.9 m, and the density ranges from 331 to 5039 stems ha^{-1} (Cao et al. 2018). Characteristics that favor the natural regeneration of *P. massoniana* include abundant seed production, ease of dispersal, and resistance to stress and some anthropogenic disturbance. In contrast, constraints to seedling establishment include environmental requirements of the species, competition, animal damage, disease and insect pests, and some anthropogenic factors, e.g., soil degradation. For example, people often excessively cut or clear *P. massoniana* forests to obtain wood or expand agricultural land. This impairs the ecology of the provenance and degrades the soil environment favorable to *P. massoniana* thereby hindering its natural renewal.

2 Deforestation or degradation of restoration sites

2.1 Site degradation

Soils, topography, and climate predispose forest sites of the Ganzhou region to degradation following certain disturbances (Figure 2). The Ultisols in Ganzhou are characterized by low organic matter content, poor soil fertility (Zhong et al. 1998), and subsoils high in sand and coarse fragments. These factors result in poor physiochemical properties that impede vegetative recovery after disturbance. Further, soil micromorphological analysis indicates that soil development is slowing as the process of iron mineralization and argillic horizon formation are gradually weakening, alteration of feldspar and mica is diminishing, and detrital weathering is intensifying (Cheng et al. 2006). Relative to topography, the terrain in the Ganzhou region is mainly composed of low mountains and hills. Where areas of sun-exposed, windward slopes occur, there is heightened potential for surface runoff and sediment transport creating highly erodible topographic conditions. Finally, the subtropical climate of the region brings high temperatures and abundant rainfall. The distribution of annual precipitation is highest in the spring and summer (70% of annual precipitation), with typhoon-induced rainstorms of high erosivity being common. This climatic pattern exacerbates severe soil erosion and degradation in the region. Together, these factors create a harsh environment for the establishment and development of *P. massoniana* forests.

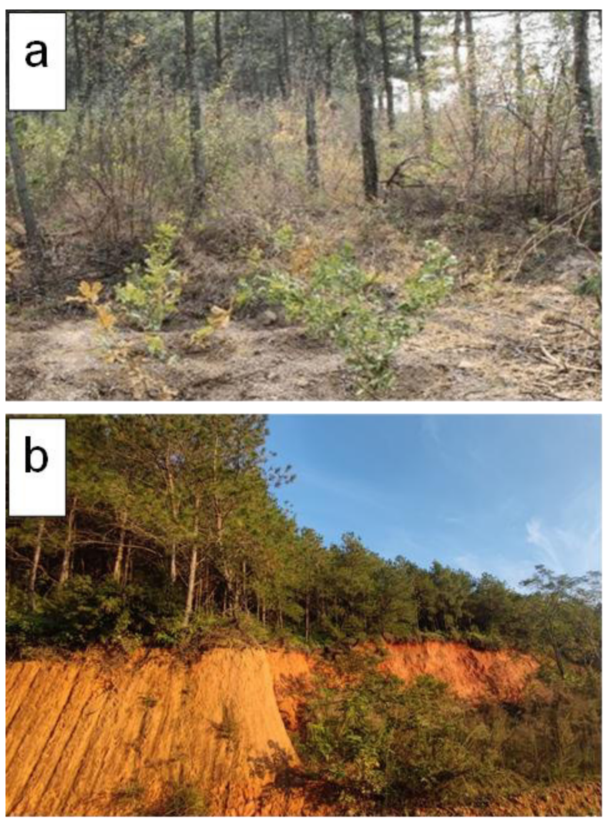

Figure 2. Degraded site (a) and soil erosion (b) in *P. massoniana* afforestation areas of Ganzhou. (Photo credits: (a) Qaio Liu, (b) FangChao Wang).

2.2 Seed, seedling, and tree damaging agents

Several diseases can impact the establishment and survival of *P. massoniana* seedlings and trees. Damping-off is a common disease caused primarily by the fungi *Fusarium oxysporum* and *F. verticillioides*. Damage occurs during seed germination near the soil surface such that the shoot may fail to emerge from the soil and die due to rot of the apical meristem or other soft tissues. Leaf blight (pathogen *Cercoseptoria pini-densiflorae*.) is common during the seedling phase, prevalent from August to October, and spreading during periods of high rain. Mortality occurs if most needles are diseased. Sphaeropsis blight (*Sphaeropsis sapinea*) can cause damping-off of seedlings or a foliar disease of larger plants (Huang 2020). Pine rust (*Cronartium quercuum*) can be harmful to established trees, creating cankers that weaken stems. Avoiding the establishment of pine-oak (*Quercus* spp. L.) mixtures when restoring forests can reduce the incidence of this disease (Liu 2021). The pinewood nematode disease (*Bursaphelenchus* xylophilus) often causes high mortality in infected trees (Kim et al. 2020). The disease is vectored by a beetle (*Monochamus alternatus*) and is commonly observed under hot and dry climatic conditions.

Animal damage to *P. massoniana* seed and seedlings mainly includes herbivory, trampling of seedlings, and other indirect damage. Rodents, e.g., squirrels (Family Sciuridae) and voles (Subfamily Arvicolinae), and birds, e.g., the Oriental magpie (*Pica serica*), often consume seed, significantly reducing its availability for germination. Large animals such as wild boar (*Sus scrofa*) and deer (Family Cervidae) can damage seedlings by browsing on the young needles, digging up the roots, or inhibiting seedling growth by destroying soil structure through trampling. In addition, gnawing by mice and rats (Family Muridae) may damage the seed coat of seed, making it easier for pathogens to infect and indirectly increasing the risk of disease.

3 Mitigating impacts for seeding

3.1 Site preparation

As seeding is conducted mostly by aerial means, site preparation is very necessary. Clearing the site of weedy vegetation is typically the first practice. Lawnmowers or brush cutters are used along the main pathways of the site for removal of herbaceous plants and small shrubs. Tractors and/or chainsaws may be needed to clear larger shrubs or dense vegetation. After vegetation is cleared, soil is loosened or tilled to prepare the seedbed. Tillers or plows are used to loosen the surface layer, especially in hardened or barren soil areas. The typical loosening depth is 10–15 cm, which enhances soil aeration and water retention. In addition, for areas with steeper slopes, bulldozers or excavators can be used to create small ditches or terraces that help control soil erosion and retain moisture. Modifying the slope through terracing can prevent seed from being washed away. Finally, aerial applications of fertilizers (such as nitrogen, phosphorus, potassium, or slow-release fertilizers), applied with helicopters or drones, can be used to improve site fertility (Chen 2022).

3.2 Damage prevention

To prevent the occurrence of disease, it is necessary to ensure that *P. massoniana* seeds are sourced from healthy origins, avoiding seed contaminated with pathogens. Additionally, necessary seed disinfection treatments should be carried out, such as soaking seed in a 0.5% potassium permanganate solution for 2 hours or spraying seed with a 3.0% formalin solution and then rinsing. Avoiding sowing densities that overcrowd seedlings is beneficial because appropriate sowing densities help maintain good air circulation around seedlings and reduces proliferation of certain pathogens. Overly dense plantations tend to trap moisture that favors the occurrence of mold and fungal diseases. In the case of severe diseases, applications of low-toxicity pesticides, such as fungicides, may be appropriate for limiting impacts. However, excessive reliance on chemical control of pathogens should be avoided, and integrated methods, including biological control and physical control, should be considered to reduce environmental pollution and to minimize negative impacts on the ecosystem. Further, regular disease monitoring should be implemented at the afforestation site, observing tree growth, leaf color, and any abnormalities in tree bark to detect potential disease risks early. Monitoring equipment, such as temperature and humidity sensors, can also be deployed to collect soil and climate data to predict and prevent possible disease outbreaks.

When selecting seed, it is important to choose *P. massoniana* varieties with strong disease resistance. Selecting superior seed sources with disease resistance can substantially limit damage caused by pathogens. Also, fertilization can promote healthy tree growth and enhance resistance to pathogens. However, excessive nitrogen fertilizer may cause trees to grow too quickly, making them more susceptible to pest damage, so fertilization should be based on soil conditions relative to the needs of the trees. Ensuring good soil drainage to prevent waterlogging is also important for minimizing damage by pathogens. Some pest prevention can be gained from the use of natural predators and other beneficial organisms. For example, releasing natural predators (such as ladybugs (Family Coccinellidae) or predatory mites (Class Arachnida) can help control pest populations. Additionally, establishing pest-resistant plants among *P. massoniana* can disrupt the spread of pests, reduce pest occurrence, and enhance the ecological stability of the forest.

Preventing animal damage on the forest restoration site has been accomplished with fencing and trapping. Fencing prevents entry of larger animals potentially damaging to the regeneration, while live traps, such as cage traps set with appropriate bait, can be established near fencing to capture smaller animals not deterred by fences. Additionally, measures to reduce animal habitat and food sources around the restoration area can be used to minimize animal damage. For example, clearing surrounding brush, decaying wood, weeds, and leaf piles can help reduce rodent habitat and the level of their presence in the afforestation area. Moreover, planting aromatic or animal-repelling plants around the *P. massoniana* forest, such as rosemary (*Salvia rosmarinus* Spenn.), mint (*Mentha* spp. L.), or lavender (*Lavandula* spp. L.), can serve as natural deterrents. These plants, through their scent or unpleasant taste, can discourage animal use of the area. The use of noise-generating devices (such as ultrasonic animal repellents) or light-based devices (such as flashing lights or mirrors) can also help scare animals away or effectively prevent animals from entering the restoration area, especially during the early stages of sowing and establishment.

4 Seed procurement and preparation

4.1 Collection

Ensuring genetic diversity of the seed source is key to enhancing the success rate of *P. massoniana* seeding. Therefore, in seeding projects in Ganzhou, the selection and management of seed sources should be an important consideration to ensure the use of high-quality seeds that are suited to local environmental conditions (Qin 2017). *P. massoniana* seed is typically collected from well-performing natural stands or orchards across the range targeted for seeding. The best time for seed collection is from mid-November to early December, with a preference for cones from trees that exhibit good growth and form. Cones harvested for their seed are usually yellow-brown or chestnut-brown and show good seed production.

4.2 Handling

Removing seed from *P. massoniana* cones is a several step process. First, the cones are screened to remove those that are broken, diseased, or infested with pests. After screening, they are sprinkled with lime and covered with straw to retain heat and moisture. Generally, a thin, even layer of lime (about 100–150 g m^{-2}) is sprinkled over the cones. The cones are turned every other day and sprayed with warm water (50 to 60 °C) for about 10 days (Lai 2019). Lastly, cones are spread on a concrete pad in the sun or heated in a ventilated room to encourage the release of the seed. Seeds that separate from cones are collected on a regular basis and prepared for storage.

Testing seed viability and quality are crucial steps for ensuring successful afforestation (Dong et al. 2019). The seed should be full, free from insect infestation, disease, and mold, and have a glossy seed coat that smells of pine resin. The kernel should be milky white, opaque, elastic, and not oily. Embryos should be bright white with more oil than the kernel; poorly developed or embryos from old seed are discolored and lack oil or appear hard, rotten, molded, or powdery. Tetrazolium chloride staining can be used as an indicator of viability—full staining of cut seed indicates viability. Quality can also be indexed by the compression method. In this technique, seeds are boiled in water for 10 minutes and then squeezed between two glass slides. White pulp squeezed out of the seed indicates good quality, while the release of water or bubbles indicates poor quality. Another test involves sliding seed across the palm of the hand with thumb and fingers of the other hand; a crisp, "rustling" sound indicates good water content (10–11%) and quality seed.

4.3 Storage and stratification

Seed separated from cones should be placed in water to remove debris and filter out bad seed; good seed will sink, and bad seed often will float. *P. massoniana* seed should be stored at 8% moisture content under controlled temperature (0 to 5 °C) and relative humidity (60% or less) (Xia 2019). Seed should be stored in moisture-resistant bags that allow for some gas exchange. The storage area should be well-ventilated to ensure adequate airing. *P. massoniana* seeds are typically stored for up to 1 year but can be stored for 2 years if adequately dried and sealed in moisture-tight plastic bags.

4.4 Plantation establishment

Aerial seeding is a quick, efficient, and low-cost method for sowing seed on afforestation sites. This method is especially suitable for seeding large, remote, and mountainous areas that are difficult to access and traverse. The area to be seeded should be a contiguous area large enough for the operation of the aircraft, i.e., helicopters or drones. Agricultural (fixed-wing planes or helicopters) aircraft were mainly used to aerially seed most of the early afforestation projects, while today some aerial seeding is being conducted with drones. Terrain and clearance should meet the operational requirements of the selected aircraft. Areas appropriate for aerial seeding of *P. massoniana* are generally hills and mountains with elevations of 300 to 800 m and slopes of less than 35°. Sites preferably are of deep, acidic red soils with good drainage and a site index of ≥16 m at base age 50 years (Zhao 2021).

In Ganzhou, aerial seeding of *P. massoniana* is typically conducted using helicopters or drones flying at a height of 50 to 100 m to ensure broad coverage of the area and minimize the impact of wind speed variation. Depending on the terrain and equipment used, about 30 to 80 ha can be seeded per hour. Given the hilly and mountainous terrain of Ganzhou, aerial seeding is an effective method for reaching remote and steep areas that are difficult to access. During the seeding process, low wind speeds are required, ideally between 3 to 5 m sec^{-1}, to prevent seed from dispersing unevenly or being blown off course. Before seeding, a terrain survey and weather assessment are necessary to ensure optimal timing and equipment settings for the seeding operation, which will improve seeding efficiency and seedling establishment rates.

Aerial seeding should be conducted between late February and early March (late winter to early spring). Because of the subtropical monsoon climate at Ganzhou, the temperature and rainfall in spring provide new germinants with a long establishment period before the hot and dry season arrives.

It is often difficult to control initial seedling density when using aerial seeding, but densities that are too high may be reduced with tending treatments after stand establishment if the area is accessible. Under normal circumstances, the seeding rate for aerially sown *P. massoniana* is 4–6 kg ha^{-1}. Densities between 3300 to 3600 stems ha^{-1} meet establishment objectives for small- to medium-diameter timber at a rotation length of 30–40 years, densities between 3000 to 3300 stems ha^{-1} meet objectives for large-diameter timber at a rotation length of 40–50 years, and densities of 1500 to 1650 stems ha^{-1} meet objectives for very large diameter timber at a rotation length of 50–60 years (Zhang 2023).

Establishing mixed-species plantations is an effective approach for enhancing the sustainability of *P. massoniana* forests. By introducing other tree species into *P. massoniana* stands, ecological diversity and stability of the forest can be improved, reducing the risks of pests and diseases that affect monocultures, and promoting soil health and water cycle improvements. For example, native evergreen species like *Quercus variabilis* Blume are highly plastic and thrive in acidic or mildly acidic soils. When established in mixed plantings with *P. massoniana*, gains are observed in forest biodiversity, soil structure, and soil water retention capacity. Two other tree species, *P. tabuliformis* Carr. and *Robinia pseudoacacia* L., are drought-resistant and are not highly demanding of soil resources. They are often used in mixed planting with *P. massoniana* to enhance stand stability and disaster resilience. Mixed-species forests of these species contribute to soil fertility, increase forest resilience, and improve carbon storage capacity. With careful species selection and planting design, mixed-species plantations can also effectively reduce the risk of forest fires, maintain biodiversity, and increase the economic value of the forest. Therefore, promoting mixed-species plantations is crucial for the long-term sustainable management of *P. massoniana* forests.

5 Post-sowing practices and plantation maintenance

Post-sowing management practices can be used on seeded sites to improve germination, seedling survival and growth, and early canopy closure. Water and nutrient management are particularly crucial. Seeded areas generally lack irrigation systems and rely on natural precipitation for stand establishment. During droughty periods, supplementation of rainfall deficits can be helpful if possible. From November to April of the following year, natural precipitation is often insufficient to meet the growth needs of seedlings, so irrigation should be conducted during this period. If the *P. massoniana* seeding area is large and includes many high slopes or hard-to-reach areas, aerial irrigation is an effective watering method. By using helicopters or drones equipped with water tanks, water can be evenly sprayed across the forest area.

Because aerially seeded sites are often infertile and seldom receive intensive site preparation, it is important to broadcast fertilizer before sowing. Applying nitrogen, phosphorus, and potassium fertilizers aerially, especially in slow-release formulations, can ensure a relatively long-term nutrient supply during the rapid growth phase of seedlings. Additional fertilization can be applied later in the rotation if deemed necessary for stand growth. Regular mechanical or chemical weeding may be required to ensure that weeds do not outcompete seedlings. Typically, large-scale weeding operations are conducted using lawnmowers or cultivators. In cases of heavy weed competition, selective herbicides can be used.

Regular inspections are necessary to detect and address pest and pathogen issues promptly. Some diseases, such as Sphaeropsis blight, can be prevented or controlled by using fungicides such as carbendazim (Huang 2020). Aerial drones can be used for large-scale pesticide applications.

Several other tending or management practices may be implemented as the stand develops. Pruning is practiced to remove dead, diseased, and overcrowded branches. Soil loosening is practiced to improve aeration and enhance root development. This is usually done before the growing season, once or twice a year, depending on the rooting depth of the trees, typically at a depth of 5–10 cm. For remote and steep sites that have been aerially seeded, soil loosening is generally more challenging due to the terrain and transportation constraints, which limit the use of machinery (Figure 3). On these sites, large-scale soil loosening is typically not done unless the terrain is relatively flat, and small equipment can be used. In practice, these remote areas often rely more on natural precipitation and subsequent maintenance measures, such as fertilization, irrigation, and weed control. Stand thinning is practiced when seedlings grow to a certain density in young and intermediate-aged stands. Trees that are poorly growing, affected by pests or diseases, or are overly dense are selectively thinned to ensure the remaining trees are healthy and disease-free. In large-scale forest areas, mechanical equipment (such as harvesters and tractors) can be used to improve efficiency, especially in flat areas. However, on steep slopes or areas with difficult access, manual thinning may be relied upon, which, although less efficient, can be effective in complex terrain.

6 Successful seeding

6.1 Defining success

Several key indicators can be considered to evaluate the success of *P. massoniana* seeding operations for forest establishment: germination rate, initial seedling establishment and plantation stocking, target species ratio, the early growth and development rate of seedlings and saplings, and seedling health (Xie 2023). These indicators, measured in plots established in the restoration area, index different aspects of plantation establishment, from seed germination to seedling growth and survival. The following paragraphs expand on each specific evaluation criteria.

Seed should germinate within a reasonable time after sowing, e.g., 2 weeks. Generally, seed germination should occur no later than 3 to 4 weeks after sowing. If germination is significantly delayed, the practitioner should review the suitability of the seed treatment methods, reassess seed quality, or determine if unsuitable environmental conditions have prevailed on the site since sowing. Delayed germination but with a germination rate greater than 60 % indicates satisfactory seed treatment and quality.

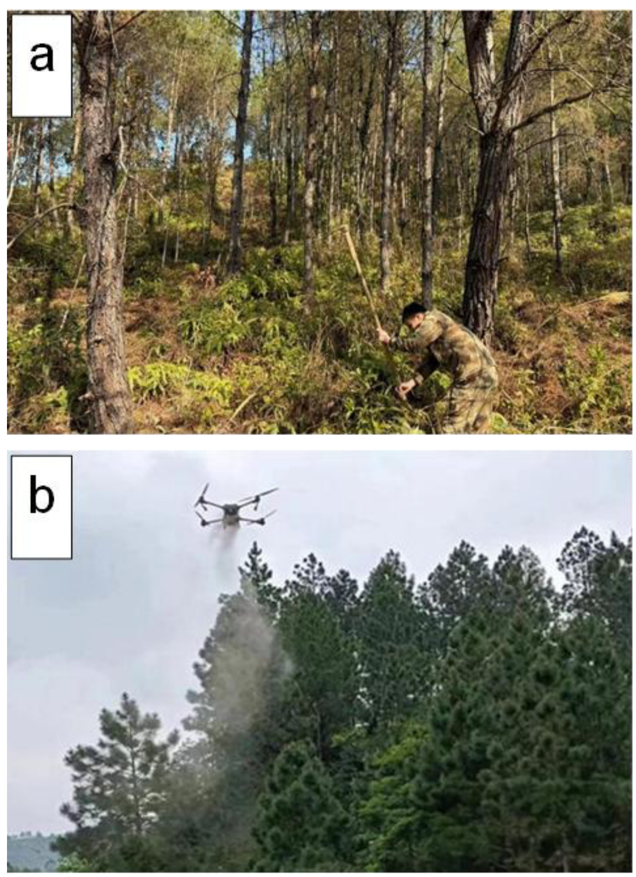

Figure 3. Soil loosening (a) and pest control (b) at *P. massoniana* afforestation sites. (Photo credits: FangChao Wang).

Initial stocking of seeded *P*. *massoniana* plantations should range from 1500 to 3600 seedlings ha^{-1}, which has been determined to be optimal for avoiding under-utilization of site resources and excessive resource competition among individuals. Along with this level of early stocking, seedling survival of 80% or greater for the first 2 years is considered adequate for plantation success. This survival rate would indicate that seed quality, plantation establishment practices, and growing conditions were conducive to stand establishment (Wu 2018, Figure 4).

Additionally, *P. massoniana* should dominate 70 to 80% of total stem density of the planting area. Several native species often naturally regenerate on seeded sites. Maintaining the targeted species ratio not only enhances the survival rate of *P. massoniana* but also contributes to ecosystem stability.

Seedlings should achieve an expected height and stem diameter within a specific growth period. One-year-old seedlings should reach a height of at least 20 to 30 cm and a basal diameter of 0.5 cm or more. Such growth would indicate sufficient nutrient and environmental conditions for *P. massoniana* success in the seeded area. Moreover, the majority of established *P. massoniana* seedlings should demonstrate consistent growth that favors desired stand development.

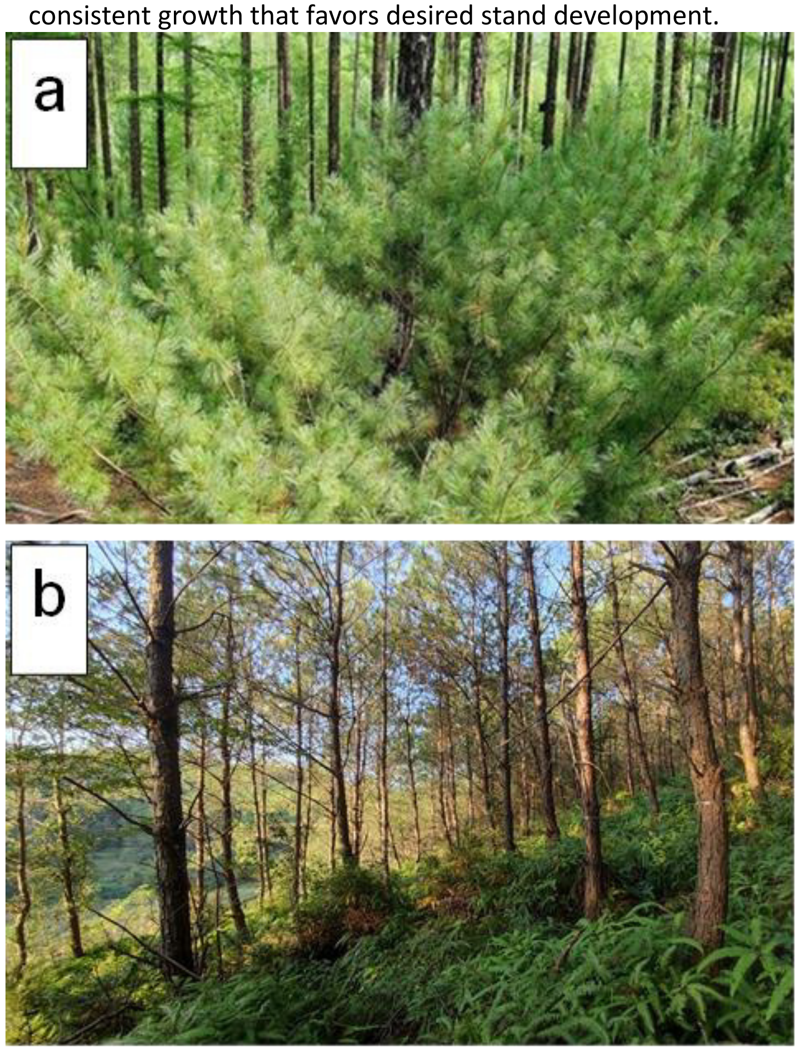

Figure 4. *P. massoniana* seedlings (a) and mature plantation (b) established through aerial seeding. (Photo credits: (a) FangChao Wang, (b) Qiao Liu).

6.2 Limiting factors and risks

To implement successful restoration of *P. massoniana* through seeding, it is important to consider factors that can limit application or add risk to seeding programs. Several factors can impact the success rate and broader application of seeding operations across the landscape. Seed quality is fundamental to success. Factors that lead to poor seed quality, such as low viability, improper storage, or inadequate seed pretreatment, can result in low germination and poor seedling health. Additionally, using seed from a limited genetic pool can reduce resilience to environmental stresses and increase susceptibility to pests and disease. Harsh site conditions that arise from various soil and site factors can hinder seed germination and seedling establishment. Soil factors limiting germination and seedling growth include soil erosion, soil degradation, poor soil drainage, droughty soil, low soil fertility, inappropriate soil pH, or unsuitable soil texture. Insufficient site preparation or plantation maintenance, such as weeding and protection from pests, pathogens, or animal damage, can result in high seedling mortality and poor growth. Finally, unpredictable, extreme weather or climatic events such as drought, frost, or excessive rainfall can negatively affect seedling survival and growth. Many seeding projects focus primarily on initial planting and survival rates, while neglecting subsequent long-term monitoring. Long-term data can help identify issues for adjustment of the management plan. Thus, proper planning with consideration for the factors that impede successful restoration is essential.

6.3 Key elements that contribute to success

Successful afforestation with seeding involves many biological, silvicultural, economic, and policy factors that must be integrated into the application. Key elements that foster successful seeding of *P*. *massoniana* to restore sustainable forests in Ganzhou include: 1) using seed of local provenance from high-quality sources that will ensure good germination and early seedling growth; 2) selecting seed sources of appropriate genetic diversity adapted to site conditions and climate in the region; 3) applying effective seed treatments such as surface sterilization and stratification to improve seed germination rate and seedling survival (Lan 2021); 4) conducting a thorough site assessment and implementing necessary site preparation such as weed control, drainage, and etc., to provide conditions conducive to germination and early seedling growth; 5) determining appropriate plantation density and intercropping plants according to ecological and economic objectives to maximize land use efficiency and tree growth space; 6) Post-sowing practices such as irrigation, fertilization, weeding, pest and disease control, and stand management (e.g., pruning, soil loosening, and thinning) are essential for ensuring seedling survival, growth, and the long-term health of *P. massoniana* plantations. Finally, regular maintenance and monitoring help effectively address challenges like nutrient deficiencies, weed competition, and pest issues (Xi et al. 2014).

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CAUTION

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8 References

Cao M, Pan P, Ouyang XZ, Zang H, Ning JK, Guo LL, Li Y (2018) Relationships between the composition and diversity of understory vegetation and environmental factors in aerially seeded *Pinus massoniana* plantations. Chin J Ecol 37(1):1–8. [In Chinese]

Chen X (2022) Planting technology and cultivation management of Masson pine. J Agric Catastrophology 12(6):170–174. [In Chinese]

Cheng DB, Cai C, Zuo CQ (2006) Advances in research of soil degradation by erosion. Res Soil Water Conserv 13(5):252–254. [In Chinese]

Ding YB (2012) Occurrence of common pests and diseases of Masson pine and their control measures. Anhui Agric Bull 18(6):97–98. [In Chinese]

Dong LJ, Wu W, Lian X (2019) Analysis of the cultivation technology of horse-tailed pine seedlings. Farmers Staff 7:102. [In Chinese]

Dou X, Deng Q, Li M, Wang W, Zhang Q, Cheng X (2013) Reforestation of *Pinus massoniana* alters soil organic carbon and nitrogen dynamics in eroded soil in south China. Ecol Eng 52:154–160. https://doi.org/10.1016/j.ecoleng.2012.12.099

Huang H (2020) Introduction to the planting and pest control technology of *Pinus massoniana*. South China Agric 14(18):76–77. [In Chinese]

Huang X, Huang C, Teng M, Zhou Z, Wang P (2020) Net primary productivity of *Pinus massoniana* dependence on climate, soil and forest characteristics. Forests 11(4):404. https://doi.org/10.3390/f11040404

Intergovernmental Panel on Climate Change (IPCC) (2023). Climate change 2021: the physical science basis. Working Group I contribution to the sixth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/9781009157896

Kim BN, Kim JH, Ahn JY, Kim S, Cho B-K, Kim Y-H, Min J (2020) A short review of the pinewood nematode, *Bursaphelenchus xylophilus*. Toxicol Environ Health Sci 12:297–304. https://doi.org/10.1007/s13530-020-00068-0

Lai X (2019) Interpretation of technical points of cultivation and planting of *Pinus massoniana*. J Green Sci Technol 7:227–228. [In Chinese]

Lan H (2021) An analysis of the technical points and popularization and application of the afforestation of *Pinus massoniana*. South China Agric 15(05):113–114. [In Chinese]

Li D (2015) Vegetation technology and economic benefit of Masson Pine. For Sci Technol Inf 4:33–35. [In Chinese]

Li M, Li H, Ding X, Wang L, Wang X, Chen F (2022) The detection of pine wilt disease: A literature review. Int J Mol Sci 23(18):10797. https://doi.org/10.3390/ijms231810797

Li QM (2023) Study on the prevention and control of common diseases and insect pests of *Pinus massoniana*. Guangdong Canye 57(05):63–65. [In Chinese] https://doi.org/10.3969/j.issn.2095-1205.2023.05.20.

Li X, Liu Q, Chen Y, Hu L, Yang F (2008) Aboveground biomass of three conifers in the Qianyanzhou plantation, Jiangxi Province, China. Front For China 3:16–23. https://doi.org/10.1007/s11461-008-0007-x

Liu L (2021) Common diseases and insect pests of Masson pine and afforestation control measures. J Agric Catastropholgy 11(12):15–16. [In Chinese]

Lou Q, Chen H, Ding G, An N (2022) Effects of afforestation density on understory vegetation and soil properties in Masson pine plantations. West For Sci 51(05):139–145. [In Chinese] https://doi.org/10.16473/j.cnki.xblykx1972.2022.05.020

Pan P, Sun Y, Ouyang X, Zang H, Rao J, Ning J (2019) Factors affecting spatial variation in vegetation carbon density in *Pinus massoniana Lamb.* forest in subtropical China. Forests 10(10): 880. https://doi.org/10.3390/f10100880

Qin GF (2017) Masson pine seed garden. China Forestry Publishing House, Beijing, China, pp 89–92.

Qin Y (2022) Exploration of planting technology and cultivation management points of Masson pine. J Green Sci Technol 1:50–52. [In Chinese]

Soil Survey Staff (2022) Keys to Soil Taxonomy, 13th ed. USDA Natural Resources Conservation Service, Washington, DC, USA.

Wu Y, Hu S, Li H (2018) Silvicultural technology of *Pinus massoniana*. Mod Agric Sci Technol 6:55. [In Chinese]

Wu Y (2019) Practical cultivation techniques of Masson pine. For Ecol 6:39–40. [In Chinese] https://doi.org/10.13552/j.cnki.lyyst.2019.06.018.

Xi W, Wang F, Shi P, Dai E, Anoruo AO, Bi H, Li W (2014) Challenges to sustainable development in China: a review of six large-scale forest restoration and land conservation programs. J Sustain For 33(5):435–453. https://doi.org/10.1080/10549811.2014.899503

Xia Z (2019) Analyzing the cultivation technology and pest management of ponytail pine seedlings. Flowers 12: 254–255. [In Chinese]

Xie H (2023) Key points of high-yield cultivation and management methods of *Pinus massoniana*. Special Econ Animals and Plants 3:137–139. [In Chinese]

Zhang HB (2023) Exploration on management of seedling afforestation of *Pinus massoniana*. Agric of Henan 23:39–41. [In Chinese]

Zhao JJ (2021) Technical points and measures of young forest nurturing in the afforestation of *Pinus massoniana*. Rural Sci Technol 12(28):85–87. [In Chinese]

Zhao L (2020) Occurrence and control of common pine diseases. J Agric Catastropholgy 10(05):23–24. [In Chinese]

Zhao X (2017) A review of technology concerning the aerial seeding afforestation in China. Shaanxi For Sci Technol 5:90–94. [In Chinese]

Zhong J, Guo QR, Luo BS, Tan J, Huang XL, Zhuo MN (1998) Study on the physical degradation and mechanism of laterite soil on sloping land–III. analysis of the mechanism of soil physical degradation. Trop Subtrop Soil Sci 7(2):166–171. [In Chinese] https://doi.org/10.16258/j.cnki.1674-5906.1998.02.015

Seeding for native afforestation in the temperate New Zealand forests

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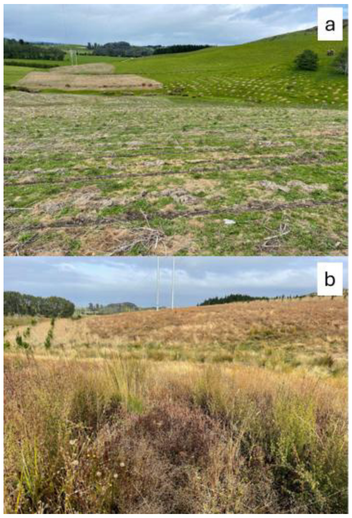

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Abstract

New Zealand supports rich temperate forests believed to have occupied up to 80% of its land area below climatic tree line prior to human arrival in the 11th century, but deforestation, particularly motivated by conversion to agricultural systems in the last 150 years, has decreased today's forest cover to less than 30% of the original estimate. There is currently interest in relatively large-scale afforestation of degraded lands, and this has initiated research and development to improve seeding of native forest species. We provide a synthesis of available literature, ongoing research, and practical experience to identify critical aspects of candidate afforestation sites, summarize practices and techniques used in current seeding research and operations, and recognize factors that affect success or failure of seeding native species. The main challenges are that pastoral farming has dramatically altered the soil microbiome, non-native mammalian herbivores and weeds reduce seedling establishment success, and many native trees are mast seeding or have recalcitrant seeds. Selection of sites with predictably adequate rainfall, deployment of fast germinating pioneer species, procurement of high-quality seed, availability of appropriate soil symbionts, and post-establishment weed and animal control are all important components of success when seeding native forest species in New Zealand.

Keywords

forest restoration, direct seeding, direct drilling, ECM, AMF, masting

Contents

1 Forests ecosystem of New Zealand

1.1 Physiographic region

The New Zealand archipelago comprises three main islands (*Te Ika o Maui*[1] North Island, *Te Wai Pounamu* South Island, and *Rakiura* Stewart Island, Figure 1) and numerous smaller islands lying mainly between latitudes 34.42° S and 47.28° S with a land area of more than 268,000 km^2. The climate is oceanic subtropical to temperate with a mean annual temperature of 16 °C in the north and 10 °C in the south. Much of New Zealand receives between 600–1600 mm rainfall annually. However, mountain ranges throughout North and South Islands intercept the predominant westerly winds to create dramatic west–east rainfall gradients. This is especially noticeable on the South Island where annual rainfall to the west of the Southern Alps can exceed 10,000 mm but some inland eastern areas receive less than 300 mm. In line with global trends, the New Zealand landmass has warmed by 0.9 °C in the last century, and 2021, 2022, and 2023 have been the hottest years on record. Climate change scenarios for New Zealand based on IPCC 6th assessment models predict temperature increases of up to 3.0 °C by 2090, an increase in severity and frequency of drought, and more extreme rainfall events (Ministry for the Environment 2024).

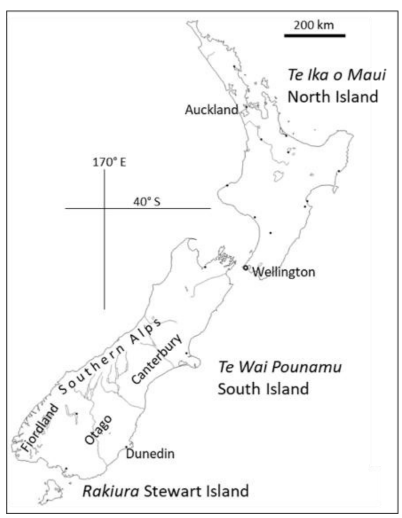

Figure 1. Map of New Zealand showing locations mentioned in the text.

[1] Indigenous Te Reo Māori place names in italics

1.2 Forest types

Prior to human arrival in the 11th century up to 80% of New Zealand's land area below climatic tree line was likely covered to some extent with conifer (Gymnosperm) and/or broadleaved (Angiosperm) forests. New Zealand native trees are overwhelmingly evergreen, unlike northern hemisphere temperate forests; only a handful of native broadleaved trees, and none of the native conifers, are deciduous. Forest composition and structure are strongly affected by elevational, latitudinal, and topographical effects on rainfall and temperature, as well as the legacy of Pleistocene glaciations on species distributions. Conifer-broadleaved forest dominated by kauri, *Agathis australis* (D.Don) Loudon (Araucariaceae), is restricted to northern North Island, along with a number of remnant representatives of tropical families. In North Island and high rainfall South Island forests, members of the Gondwanan conifer family, Podocarpaceae, are often emergent over a diverse broadleaved canopy made up of species in families such as: Araliaceae, Cunoniaceae, Elaeocarpaceae, Lauraceae, Malvaceae, Myrtacaeae and Pittosporaceae. These forests also support an abundance of ferns, vines, and epiphytes, making them structurally more similar to tropical rainforests than northern hemisphere temperate forests. Evergreen forests of *Fuscospora* and *Lophozona* species (southern beeches, Nothofagaceae) dominate in drier and colder parts of New Zealand, as well as extremely high rainfall areas such as Fiordland, often growing in near monoculture. Prior to the arrival of humans, fire was not a frequent occurrence; the most common disturbances were likely windthrow, flooding and landslides, with geothermal activity and volcanism affecting central parts of North Island (Veblen et al. 2016).

1.3 History of deforestation and degradation

Like the rest of the world, human activities in New Zealand have resulted in large scale deforestation such that < 30% of pre-human forest cover remains today (Ewers et al. 2006). Unlike the rest of the world this deforestation has occurred in little more than 800 years, as New Zealand was the last major landmass to be permanently inhabited by humans. Losses have accelerated over the past 150 years, during which time half of the land area below the tree line has been converted into agricultural systems. Furthermore, New Zealand is unique among temperate forested lands globally in that native forests did not evolve with grazing mammals; the only mammals native to New Zealand are marine mammals and bats (suborder Microchiroptera). A large suite of introduced mammalian grazers, browsers, and seed predators have become naturalized in native forests following the arrival of humans (King 1990), causing considerable ecological damage (e.g., Wilson et al. 2006). These species include seven species of deer (Family Cervidae), feral pigs (Family Suidae), feral goats, chamois and Himalayan Tahr (all Family Bovidae), Australian brush-tailed possum (*Trichosurus vulpecula*), European rabbits and hares (Family Leporidae), house mice and three rat species (Family Muridae). In addition, domestic livestock such as cattle and sheep (Family Bovidae) penetrate and damage native forests.

2 Critical aspects of candidate afforestation sites

2.1 Site factors

Site factors such as microclimate, water availability, legacy soil conditions, and accessibility for machinery are critical determinants of the design and success of any direct seeding operation. Sites available for native afforestation in New Zealand are typically on rugged, marginal, or remote land otherwise unprofitable for agriculture or commercial forestry, or which has been damaged by erosion or flooding. Afforestation with native species is also a desirable outcome following large-scale weed control operations, such as aerial herbicide application to control dense infestations of invasive northern hemisphere conifers, especially in inland South Island. Seeding with mechanical seed drills is of limited use for afforestation in these situations due to the difficult terrain and abundance of coarse woody debris. Aerially dispersed seed balls hold more promise for establishing native forest species into these types of sites (Griffiths et al. 2025).

2.2 Soil factors and root symbionts

Pastoral farming has significantly modified New Zealand's soil environment in the process of converting forested ecosystems to a grass (Poaceae) dominated landscape. As a result, the structure, chemistry and biology of soils in areas available for afforestation are far from what they would have been prior to deforestation. In particular, the availability of beneficial symbionts such as mycorrhizal fungi is very different in a pasture compared with a virgin native forest. Unlike other temperate regions, the majority of native trees in New Zealand form associations with arbuscular mycorrhizal fungi (AMF) (Orlovich and Cairney 2004). For example, kauri is associated with a high diversity of AMF taxa, as is the 'At Risk' myrtaceous tree *Lophomyrtus bullata* Burret (Padamsee et al. 2016; Ford et al. 2023). However, AMF communities can differ substantially between co-occurring native and non-native species in New Zealand (Ramana et al. 2023), so pastoral soil microbiomes may not be suitable for native AMF-dependent tree species (Horton et al. 2024).

Only members of the southern beech family, Nothofagaceae, are exclusively ecto-mycorrhizal (ECM), and two widespread pioneer tree species, mānuka (*Leptospermum scoparium* J.R.Forst. & G.Forst.) and kānuka (*Kunzea ericoides* (A.Rich.) Joy Thomps. *sensu lato*) both Myrtaceae, are able to form associations with both ECM and AMF (Teste et al. 2020). Molecular analyses of ECM associated with southern beech shows host specialization among the five native species (van Galen et al. 2023a), and limited overlap with ECM taxa found on introduced trees (Orlovich and Cairney 2004; Teasdale et al. 2012). Likewise, Kōwhai species (*Sophora,* Fabaceae) form associations with specific native nitrogen-fixing *Mesorhizobium* bacteria, rather than introduced *Rhizobium* strains associated with pastural legumes (Tan et al. 2015). This reliance on native soil symbionts creates additional issues when attempting to (re)establish native forest species on ex-agricultural land.

2.3 Competition from non-target plant species

Competition from existing vegetation, and weeds present in the soil seed bank, is one of the biggest obstacles to successful native afforestation in New Zealand, especially on ex-agricultural land (Ledgard et al. 2008). During the process of clearing New Zealand native forests for farming a vast array of pastural grasses, forbs, and agricultural weeds were introduced and became naturalized in the landscape. When unmanaged, these species redirect natural successional processes and outcompete native seedlings (McQueen et al. 2006). In addition, woody weeds can be problematic when grazing pressure from feral or domestic stock is removed. For example, the woody leguminous shrubs gorse (*Ulex europaeus* L.) and broom (*Cytisus scoparius* (L.) Link) are widespread weeds of unmanaged agricultural lands especially in central and southern New Zealand and aggressively spreading naturalized northern hemisphere conifers affect c.1.7 million ha of agricultural and conservation land, mainly in eastern South Island (Wotton and McAlpine 2013).

3 Mitigating impacts for seeding

3.1 Site selection and preparation

An integral aspect of site preparation in New Zealand is the control of pre-existing herbaceous vegetation that could outcompete slower-growing natives. A common approach involves one or more applications of a broad spectrum herbicide. However, repeated broad spectrum herbicide treatments may have unintended negative consequences for soil microbiota (Helander et al. 2018). Non-herbicide methods such as scraping to remove the topsoil and the associated weed seed bank, followed by ripping to loosen the substrate, have been trialed at small scales in New Zealand and have potential value, as some native woody species establish well following soil disturbance (e.g., Allen et al. 1992; Ledgard et al. 2008). Plowing or ripping can be beneficial because it increases seed-soil contact and the extent to which seeds can imbibe water; these practices also alleviate soil compaction and help to eliminate resident vegetation (Ruthrof et al. 2013; Brown et al. 2023). The addition of woody debris may also aid in seedling establishment due to the creation of specialized microsites (Shemesh 2024).

3.2 Damage prevention

Successful forest restoration in New Zealand requires the removal or control of domestic livestock and feral browsers that damage native seedlings. For small to moderate sized projects this could involve fencing, but aerial or ground culling, as well as targeted poison operations such as rabbit control with Pindone [2-(2,2-dimethyl-1-oxopropyl)-1H- indene-1,3(2H)-dione], can provide adequate release from browsing pressure at large scales. Nurse crops can also aid native tree establishment by not only providing shelter but also restricting livestock access to seedlings. In a number of southern New Zealand studies, gorse has been shown to successfully shelter native trees establishing from seeds, eventually senescing as it is overtopped and shaded by the developing native canopy (Wotton and McAlpine 2013). Trials are also underway to investigate using areas of native bracken fern (*Pteridium esculentum* (G.Forst.)

Cockayne) to provide shelter and reduce browsing damage to native trees establishing from seed.

4 Seed procurement and preparation

4.1 Seed availability and eco-sourcing considerations

Lack of native seed supply is a significant impediment to seeding across New Zealand (Douglas et al. 2007). Natural seed sources and their associated genetic diversity have been depleted with the conversion of virgin forests into agricultural land over time (Norton et al. 2018). In addition, many native trees are bird (class Aves) pollinated and there is evidence that reductions in bird populations are affecting seed quantity and quality for some species (Anderson et al. 2020). The frequency of dioecy (separate male and female trees) and gynodioecy (separate female and hermaphrodite trees) is also unusually high among native New Zealand trees, meaning that effective population sizes are further reduced and only a limited number of trees can be relied on to provide high quality out-crossed seeds. Seed supply for afforestation in New Zealand is further complicated by the high frequency of masting among native trees including most of the southern conifer family Podocarpaceae, the southern beeches, and other key broadleaf species. These features of the native woody flora create particular challenges for seed collection and supply. However, the ability to predict heavy mast years from annual temperature differences of successive years (Samarth et al. 2020) now means seed collection efforts, e.g. positioning of nets under female trees, can be upscaled when seed is likely to be abundant. For tree species that reproduce annually, the seasonality of fruit maturation is fairly well known. For some species, fruit linger for some time on trees, e.g. many populations of the pioneer species mānuka exhibit serotiny, so capsules can be collected at any time of the year and heated to release the minute seeds. However, for fleshy-fruited trees, fruits are often rapidly removed by birds, so collection has to be well timed.

Due to the fragmented nature of the remaining natural forests, limited areas are available from which to collect locally appropriate, 'eco-sourced' seeds. Furthermore, there is evidence in New Zealand that small population sizes can lead to significant inbreeding depression in some tree species, meaning that local remnants may not produce any high-quality seeds (e.g., Robertson et al. 2011). Luckily, recent studies have demonstrated that there are low levels of regional genetic differentiation in many native trees, especially on South Island (Heenan et al. 2023), so seeds can legitimately be sourced from a wider area to maximize the genetic diversity of seeds being sown. Sourcing seeds from a wider area also allows practitioners to plan for climatic resilience via climate-adjusted provenancing (Prober et al. 2015), as forests established currently will very likely face challenging changes in rainfall and temperature regimes for decades to come.

4.2 Seed handling, cleaning and pre-treatment

Fleshy fruits are especially common among New Zealand native trees (Lord 1999) with the pulp containing germination inhibitors. Many species also have hard, thick seed coats. Standard seed pretreatments, including pulp removal, moist cold stratification, and scarification for hard coated seeds, have increased the ability to efficiently germinate a range of New Zealand native tree species employed in afforestation (Metcalf 2007; Rowarth et al. 2007). Most fleshy-fruited species can be quicky cleaned in large quantities by floating them in water and agitating with a stab blender then pressing through a sieve. The germination of some species is also improved if flesh was left to rot off prior to sowing. Species with plumed or sticky seeds, such as *Pittosporum* Banks ex Gaertn. (Pittosporaceae) and *Olearia* Moench (Asteraceae) need to be treated before they are suitable for broadcasting or drilling. *Eucalyptus* L'Hér. oil has been successfully used as a pre-treatment to remove sticky residue from *Pittosporum* seeds (Table 1).

Research into the effects of chemical or hormonal treatments on germination rates of native species are still in their earlier stages, but there are some promising indications that gibberellic acid and potassium nitrate seed pre-treatments, can overcome seed dormancy for some species, and seed priming with sodium chloride and hydrogen peroxide can improve cumulative germination and germination rates for others (Moss-Mason 2024).

Table 1. Native New Zealand trees and shrubs used in direct seeding trials. Superscript 1: Overdyck et al. (2013); 2: Lord unpublished data (*Ngā Kākano Whakahau* project)*;* 3: estimates from Dodd and Power (2007); 4: Griffiths et al. (2025); 5: mean and maximum in short/long grass from Ledgard et al. (2008); 6: van Galen et al. (2022).

Species	Seeding method trialled	% Germination in field trials (FT) and/or viability tests (C)	Factors improving germination and establishment in the field
Beilschmiedia tawa (A.Cunn.) Benth. et Hook.f. ex Kirk	Seed balls[1]	FT 59%	Remove flesh, recalcitrant, sow fresh
Coprosma propinqua A.Cunn., Mingimingi (Rubiaceae)	Hand-Broadcast, Burford Tree Seeder, Cross-slot drill[2]	FT <1%, C: >10%	Remove flesh, moist stratify, control weed and grass regrowth
Coprosma robusta Raoul, Karamu (Rubiaceae)	Hand-Broadcast[3] Seed balls[4]	FT <5%, C >50%	Remove flesh, stratify in moist sand for 2 months
Cordyline australis (G.Forst.) Endl., Tī Kōuka (Asphodeliaceae)	Burford Tree Seeder[2]	FT <1%, C >10%	Remove flesh, moist stratify, best in moister sites
	Hand-Broadcast[5]	FT mean 5.4/8.3%, max 20/50%	
	Seed balls[4]	C >90%	
Corokia cotoneaster Raoul, Korokia (Argophyllaceae)	Burford Tree Seeder, Cross-Slot drill[2]	FT 0%, C 0%	Known to require after-ripening. Needs more work on seed biology
Dacrydium dacrydioides (A.Rich.) de Laub., Kahikatea (Podocarpaceae)	Enviromulch[2]	FT 0%, C 0%likely seeds desiccated	Collect in heavy mast year, recalcitrant, AMF, more research needed
	Seed balls[4]	FT 0%, C >10%	
Entelea arborescens R.Br. (Malvaceae)	Seed balls[4]	C >50%	
Fuscospora cliffortioides (Hook.f.) Heenan et Smissen, Mountain Beech (Fagaceae)	Hand-broadcast[6]	FT >10%, C >10%	Collect in heavy mast year, best sown fresh, shelter during establishment, control weed and grass regrowth, ECM
	Burford Tree Seeder[2]	FT <1%, C <10%	
	Triple Disk drill[2]	FT 0%, C <10%	
Fuscospora solandri (Hook.f.) Heenan et Smissen, Black Beech (Fagaceae)	Hand-broadcast, Burford Tree Seeder[2]	FT <1%, C >10%	
	Cross-Slot drill[2]	FT 0%, C >10%	
	Enviromulch[2]	FT <10%, C >10%	

Fuscospora truncata (Colenso) Heenan et Smissen, Hard Beech (Fagaceae)	Seed balls[4]	C <10%	
Griselinia littoralis Raoul, Kapuka (Griseliniaceae)	Enviromulch[1]	FT <1%, C >10%	Remove flesh, sow fresh or moist stratify, recalcitrant, AMF
	Hand-Broadcast[3]	FT mean 7.9/10.4%, max. 35/40%	
Hoheria angustifolia Raoul, Houhere (Malvaceae)	Burford Tree Seeder[1]	FT >10%, C >10%	Control weed and grass regrowth
Kunzea ericoides (A.Rich.) Joy Thomps., Kānuka (Myrtaceae)	Hand-broadcast, Burford Tree Seeder[1]	FT >10% C >50%	Control weed and grass regrowth, shade-intolerant, drought tolerant once established, thrives in gravel, AMF/ECM
Leptospermum scoparium J.R.Forst. & G.Forst., Mānuka (Myrtaceae)	Enviromulch, Hand-broadcast, Burford Tree Seeder[1]	FT >10%, C >10%	Control weed and grass regrowth, does not tolerate shade or drought, often seeds after fire, AMF/ECM
	Cross-slot drill[1]	FT <1%, C >10%	
	Seed balls[4]	C >10%	
Lophozona mensiezii (Hook.f.) Heenan et Smissen, Silver Beech (Fagaceae)	Burford Tree Seeder, Cross-Slot drill[1]	FT 0%, C 0%	Collect in heavy mast year, sow fresh or moist stratify, ECM
	Seed balls[4]	C >10%	
Melicytus ramiflorus J.R. & G. Forster, Mahoe (Violaceae)	Hand-Broadcast[5]	FT mean 2.5/2.9%, max. 10/25%	Remove flesh, stratify in moist sand for 2 months
Myoporum laetum G. Forst., Ngaio (Scrophulariaceae)	Hand-Broadcast[5]	FT mean 4/0%, max. 5/0%	Remove flesh, stratify in moist sand for 2 months
Myrsine australis A.Rich, Red Mapou (Primulaceae)	Hand-Broadcast[5]	FT 0/0%	Remove flesh, stratify in moist sand for 2 months
Phormium tenax J.R.Forst. & G.Forst., Harakeke (Asparagaceae)	Enviromulch[2]	FT >10%, C >50%	Control weed and grass regrowth, moist stratify, best in moist soils
	Hand-Broadcast[5]	FT: mean 6.7/2.1%, max. 25/10%[3]	
Pittosporum eugenioides A.Cunn., Tarata (Pittosporaceae)	Hand-broadcast, Burford Tree Seeder, Cross-slot drill[2]	FT 0%, C 0%	Remove sticky aril with *Eucalyptus* oil, control weeds and grass regrowth, delayed germination typical
Pittosporum tenuifolium Banks & Solander. ex Gaertn., Kohuhu (Pittosporaceae)	Hand-Broadcast[5]	FT mean 12.9/16/7%, max. 60/50% in disturbed plots	
Podocarpus totara G.Benn. ex D.Don, Tōtara (Podocarpaceae)	Burford Tree Seeder[2]	FT <1%, C >10%	Collect in heavy mast year, moist stratify, AMF
	Seed balls[4]	C <10%	
Pseudopanax arboreus (L.f.) K.Koch, Five Finger (Araliaceae)	Enviromulch, Burford Tree Seeder[2]	FT 0%, C 0%	Remove flesh, needs more work on seed biology
	Hand-Broadcast[5]	FT mean 0/0.8%, max. 0/20%	
Solanum aviculare G.Forst., Poroporo (Solanaceae)	Hand-Broadcast[5]	FT mean 10.4/2.5%, max. 45/15%	Remove flesh, stratify in moist sand for 2 months
Sophora microphylla Aiton, Kōwhai (Fabaceae)	Hand-broadcast, Burford Tree Seeder[2]	FT >50%, C >90%	Scarify or nick. Seedlings vulnerable to rabbits, killed by clopyralid herbicides, *Mesorhizobium*
	Cross-slot drill[2]	FT 0%, C >90%	
	Hand-Broadcast[5]	FT mean 3.8/7.5%, max. 15/40%	

	Seed balls[2]	C >90%	
Veronica salicifolia G.Forst., Koromiko (Plantaginaceae)	Burford Tree Seeder[2]	FT >10%, C >50%	Control weed and grass regrowth, sensitive to clopyralid herbicides
	Cross-slot drill[2]	FT 0%, C >50%	
	Seed balls[4]	C >90%	
Veronica stricta Banks & Sol. ex Benth., Koromiko (Plantaginaceae)	Hand-broadcast[3]	FT <1%, C >50%	

4.3 Seed storage

Knowledge gaps concerning native seed storage and germination requirements are apparent across many native tree taxa in New Zealand (Douglas et al. 2007; Metcalf 2007). It is thought that the majority of the flora produce orthodox seeds that can be stored for prolonged periods at reduced moisture content (Wyse et al. 2023). However, the seeds of some key native trees, including many native conifers, are recalcitrant, meaning they lose viability once dry and cannot be easily stored (Rowarth et al. 2007; Wyse et al. 2023). Detailed experimentation is needed for such species to determine optimal seed storage and germination conditions (e.g., van der Walt et al. 2020). Recalcitrance, combined with the fact that masting behavior is common among New Zealand trees (Webb and Kelly 1993) means that viable seed for some key tree species is only available in sporadic years and must be sown fresh for best effect.

5 Seeding methods in New Zealand

New Zealand has historically used aerial seeding to establish introduced conifers in remote hill country to combat accelerating erosion (Faulkner et al. 1972). However, seeding of native species is still the subject of research and development with very few large-scale projects implementing seeding for native afforestation. Douglas et al. (2007) reviewed the use of seeding for restoration in New Zealand and concluded that its applicability was constrained at that time by a lack of seed supply, knowledge of best-practice sowing times and rates, unreliable germination and seedling development, and competition from environmental weeds. For 10 years following the publication of that review only two seeding trials were attempted. Ledgard et al. (2008) trialed seeding into seven ex-pasture environments in Canterbury, New Zealand, using hand broadcasted seeds of 23 native tree and shrub species. They concluded that soil disturbance paired with herbicide application prior to seeding positively influenced the establishment of native species. At that time only one study on private land involving agricultural machinery had been conducted, which successfully established *L. scoparium* into plowed furrows (Ledgard et al. 2008).

5.1 Species composition and sowing density

Almost all trials to date have included a mix of nurse or pioneer species with late successional stage species in seed mixes. Nurse species have included agricultural crops such as annual oats (*Avena sativa* L.) and narrow-leaved plantain (*Plantago lanceolata* L.) that could provide some shelter for native tree seedlings but not compete with them. Native pioneer species have also been targeted in trials and proven to cope with most conditions. Sowing densities are conditional on application method but in most cases aim to ideally establish one surviving tree for every c. 2–3 m^2, i.e., a density of 3000–5000 stems ha^{-1}.

The inclusion in seed mixes of nurse species that germinate and grow rapidly to create a canopy is an effective means to control non-target species, particularly vigorous grass regrowth. Studies in southern New Zealand have successfully used the large bunchgrass toetoe (*Austroderia richardii* (Endl.) N.P.Barker et H.P.Linder, Poaceae), mānuka, kānuka, and koromiko (*Veronica* spp. L.) to rapidly create shade (Table 1). Many large-seeded, late successional tree species such as members of the Podocarpaceae and Lauraceae germinate slowly and over an extended period of time. Pioneer species can create conditions suitable for the emergence and survival of these slower-germinating, late successional trees species, which can either be introduced to the site along with fast growing pioneer species, or oversown at a later date once a preliminary woody canopy has formed. Seeding experiments by Paul et al. (2020) indicate that some experimentally sown large-seeded species can remain in the soil for more than a year and still emerge and establish. The inclusion of the dual mycorrhizal species mānuka and kānuka in seed mixes also provides potential hosts for ECM as well as AMF fungi, creating conditions that may facilitate the establishment of southern beech species (Nothofagaceae) which are obligately dependent on ECM fungi.

For species that require the formation of mycorrhizae for successful establishment, eco-sourced fungal spores or forest duff (litter layer, O, and uppermost A soil horizons) can be introduced along with seeds. For some New Zealand ECM fungi, spores from dried fungal fruiting bodies can remain viable and germinate after more than 120 days storage, providing a means of collecting and storing identified fungi for later use as inoculum (Bohorquez et al. 2019).

5.2 Sowing practices

Seeding via a range of methods has been the focus of a New Zealand government funded research project running from 2019–2024: *Ngā Kakano Whakahau: The Seeds Project*, led by the first author. This project aimed to test and refine seeding approaches for establishing native forest at scale on retired pasture in South Island, in conjunction with the delivery of beneficial mycorrhizal fungi to remediate soil microbiomes in deforested landscapes. Initial trials aimed to compare the cost vs. success of a range of seed application methods including hand broadcasting seeds, seed application within a mulch matrix, and direct drilling using a purpose-built tree seeder and agricultural seed drills. Some trials have already been published or made available as theses (e.g. Bohorquez et al. 2021; Van Galen et al. 2022; Barber-Sperling 2023; Strawsine et al. 2024; Horton et al. 2024). Additional results of the program are presented in the following sections.

5.2.1 Direct drilling

Advances in direct drilling for afforestation in Australia led to a consortium of interested parties importing an Australian invention, the Burford Tree Seeder, into New Zealand in 2016. Developed in South Australia by Rod Burford, the Burford Tree Seeder has been used for restoration in Australian shrub and grasslands, with generally high success (Streatfield 2019). The Burford has a single disc coulter that scalps a furrow of varying width, then seeds are deposited at a specified depth within the furrow via a single tine. Seed size determines the ideal seeding depth; larger seeds benefit from

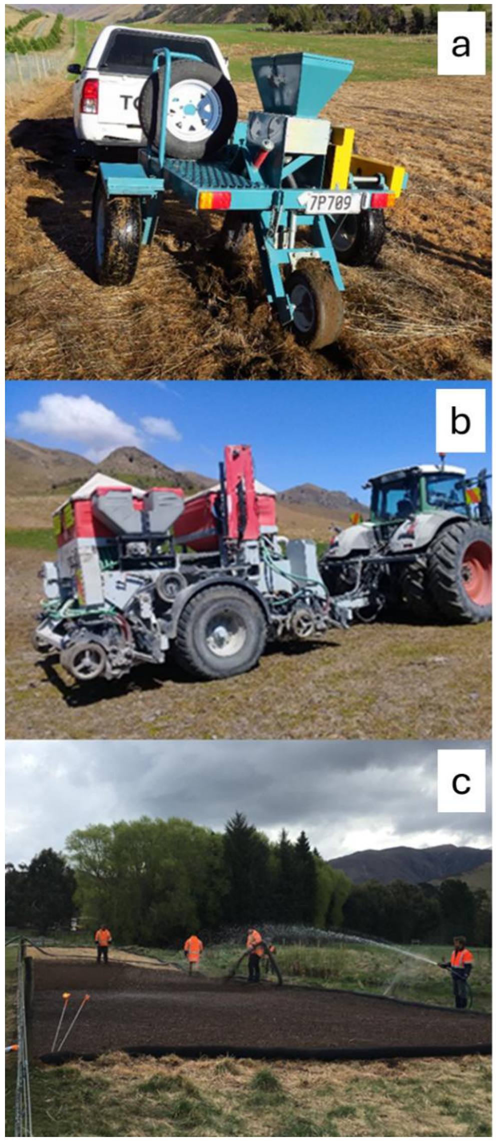

Figure 2. (a) Burford Tree Seeder being towed by a 4-wheel-drive vehicle; (b) Cross-Slot™ agricultural drill towed by a tractor; (c) Enviroblanket™ Mulch application (Photo credits: Janice Lord).

burial no deeper than two times the size, whereas smaller seeds are better suited to placement on top of the soil surface (Bewley and Black 1994). Two separate seed hoppers on the Burford can deliver small and large seeds independently, so that while large seeds are sowed at depth by the tine, small seeds can be deposited on the surface of the furrow base and pressed into the ground with the press wheel. Also, as tillage, in the form of scalping a furrow, coincides with seed drilling, no prior cultivation is required, however, considerable site preparation in the form of repeated herbicide applications is recommended to reduce competition from weeds (Streatfield 2019). The Burford most effectively drills on bare land with no thatch or rocks and can only be used where 4-wheel-drive (4WD) vehicle access is safe, making it inappropriate for hilly, wet, or stony landscapes (Figure 2). However, the size of the Burford makes it easily transportable between sites. In recent years, multiple trials with the Burford Tree

Seeder, facilitated by the New Zealand Department of Conservation and more recently the commercial enterprise SeedNZNatives (https://www.seednznatives.co.nz), have been established in southern and eastern South Island (e.g., Figure 3). Best results from seed drilling trials in southern New Zealand using the Burford Tree Seeder have been for areas sown in spring on ex-agricultural sites that had been prepared with two herbicide applications in the previous spring and autumn. In areas with milder winters, autumn establishment can provide seeds with natural moist stratification conditions. All sites also had two follow-up selective herbicide applications to control weed regrowth (Streatfield 2019).

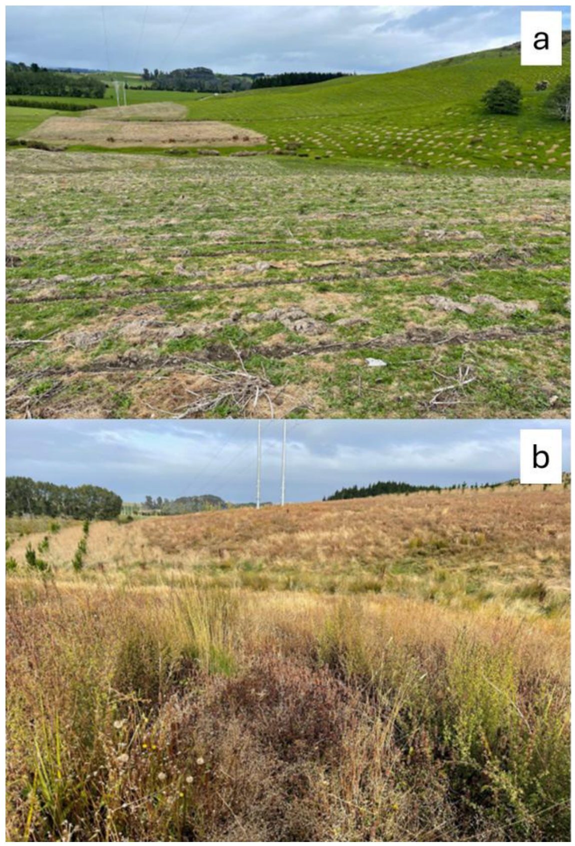

Figure 3. Native tree corridor sown under power lines with Burford Tree Seeder between areas planted with *Pinus radiata* D.Don, Table Hill, Otago. (a) Immediately after sowing, 29 October 2021; (b) 17 month old mānuka (*Leptospermum scoparium* J.R.Forst. & G.Forst.) and tī kouka (*Cordyline australis* (G.Forst.) Endl.) indicated, 29 March 2023 (Photo credits: Pieter Britz, Seed NZ Natives Ltd.).

As part of The Seeds Project, the Burford Tree Seeder was compared with two conventional agricultural drills – the Cross-Slot^{TM}, a no-till precision drill developed in New Zealand (Figure 2), and a standard triple disk drill (Lord, unpublished data). The same native seed mix was sown using the Burford Tree Seeder and the Cross-slot drill on 2 ha of retired cropping and pasture in inland Canterbury, South Island. The 4WD vehicle towing the Burford Tree Seeder was unable to navigate the rocky sloped areas accessible to the tractor towing the Cross-Slot drill, so some differences between sown areas were unavoidable. The standard triple-disk drill was trialed at a separate site in inland Otago, South Island, with a less species diverse seed mix. Both the Cross-slot drill and Burford Tree Seeder were capable of delivering small amounts of seeds over the study area. However, the triple disc drill required a minimum of 15–20 kg of seed to be operational regardless of the size of area to be drilled. In that trial we used 4 kg of native tree seed supplemented by 16 kg of annual oats, which was an economic solution to the issue of seed volume. Inviable granular material such as processed rice (*Oryza sativa* L.) or sand (e.g., Otago South Rivercare 2024) could also be effective at adding volume to native seed mixes without introducing additional species that might compete with native species.

We had expected that the no-till Cross-Slot might result in lower weed regrowth as it does not turn a furrow, instead it deposits seeds to a precise depth within an inverted T-shaped slot cut directly into the soil and closed over with a press wheel. However, weed regrowth did not differ significantly between drill types. Seedling emergence and survival was higher in the Burford Tree Seeder area than in the areas sown with the agricultural drills, likely because the variability in deposition depth, and also the creation of a heterogeneous germination tilth in the furrow provided a greater variety of microsites that would suit a mixture of species.

5.2.2 Pneumatic seeding within a mulch matrix

The EnviroBlanket^{TM} Mulch seeding method, developed and implemented by RedTree Environmental solutions (https://redtree.co.nz/) consists of a custom blended mulch applied aerially or under pressure together with a site-specific mixture of native seeds (Figure 2). As part of The Seeds Project in inland Canterbury, Enviroblanket trials were applied along a riparian strip unsuitable for vehicle access (Lord, unpublished data). The site was prepared with two applications of broad spectrum herbicide several months before trial establishment. A thick layer of mulch was first deposited on the site as a weed suppressant, then a thin layer of mulch and seeds added. Trials were initially watered to help compact the mulch but not watered thereafter. Some seedlings of pioneer species emerged from the EnviroBlanket mulch, but none survived beyond the first year. The reasons for this were most likely that weeds were not adequately controlled prior to establishment or during the trial, and the species sown were not able to tolerate the severe site conditions over the ensuing 18 months—a very dry summer, followed by a very cold winter. While this method has proven useful for revegetating difficult access sites lacking in germination microsites (e.g., exposed rocky slopes), it was not cost effective for large-scale afforestation on retired agricultural soils with a large residual weed seed bank.

5.2.3 Aerial seeding

Aerial seeding using a mixture of seeds and ballast such as sand or rice, or using seeds encapsulated into balls, allows desirable species to be introduced into otherwise inaccessible areas, or into disturbed sites after events such as wildfires and landslips cost-effectively (Xiao et al. 2015; Griffith et al. 2025). Seeding native species aerially has been receiving increasing attention in New Zealand. In 2022, the Otago South Rivercare group trialed aerial seeding combined with stock trampling and follow-up weed control with aerially applied herbicide. Two years after the trial, a range of herbicide tolerant species had successfully established, and additional trials are ongoing (Otago South Rivercare 2024). Aerial seeding has also been the focus of a recent project funded by the New Zealand Ministry for the Environment involving the authors, the New Zealand

Department of Conservation, and the commercial drone company Envico Technologies (https://www.envicotech.co.nz/). Pioneer species such as mānuka, kānuka, koromiko, and toetoe, as well as the monocotydonous tree tī kōuka (*Cordyline australis* (G.Forst.) Endl., Asparagaceae) and the broadleaved trees kōtukutuku (*Fuchsia excorticata* (Forst. & Forst. f.) L. f., Onagraceae) and poroporo (*Solanum aviculare* G.Forst.,Solanaceae) show promise for large-scale dispersal via seed balls. Formulation, viability, and dormancy issues still require more work for larger-seeded and/or late successional tree species to be established via this method (Griffiths et al. 2025; Lord et al. 2025).

6 Post-sowing practices and maintenance

While initial shelter seems to improve seedling survival, post-emergence weed control is critical to establishment, especially control of the vigorous regrowth of introduced pasture grasses and clovers (*Trifolium* spp. L.) in ex-agricultural sites. Targeted herbicides such as haloxyfop-P and clopyralid have proven particularly effective for controlling competition from grasses and clovers (van Galen et al. 2022), but obviously these would have negative impacts on sensitive native grasses and legumes. Furthermore, the long-term impacts of herbicide use on native plants and soil microbiota is still unknown. Due to the damage that introduced herbivores such as hares, rabbits, deer, and Australian brush-tailed possums inflict on the regeneration of native species, an integrated pest control plan involving fencing, trapping, shooting, and or poisoning needs to be included as a central focus of seeding operations (Forbes et al. 2020).

7 Factors affecting success and failure

Fast germinating pioneer species are more amenable to seeding efforts, due to their ability to establish rapidly in fluctuating field conditions (e.g., Figure 3). Woody pioneer species currently known to be suitable for establishment from seed at large scales in temperate New Zealand include mānuka, kānuka, *Hoheria* spp. A.Cunn., *Plagianthus* spp. J.R.Forst. & G.Forst., whau (*Entelea arborescens* R.Br.) (three Malvaceae trees), and koromiko, due to seed availability, viability, and ease of handling. However, small-seeded species such as mānuka and kānuka, which naturally germinate after soil disturbance, appear less able to tolerate competition from resident vegetation, especially from dense mats of introduced pasture grasses and clovers, so post-establishment weed control is imperative. Among larger-seeded or late successional tree species, seeding trials in southern New Zealand (e.g., Ledgard et al. 2008; Streatfield 2019; Paul et al. 2020; Barber-Sperling 2023; van Galen et al. 2024) have had some success with freshly collected, as well as moist stratified, mountain beech (*Fuscospora cliffortioides* (Hook.f.) Heenan et Smissen), cleaned and stratified tī kōuka, *Coprosma* J.R.Forst. & G.Forst. (Rubiaceae), *Pittosporum* spp., and scarified kōwhai (*Sophora* spp. L., Fabaceae) (Table 1). More research is needed on other large-seeded native New Zealand species. Potential also exists to transition non-native forests to native forests using the non-native canopy as a nurse crop to suppress competing vegetation, as many native woody species can establish under non-native canopies (Pritchard et al. 2024).

Success is also dependent on the availability of high-quality seed, which is limited to mast years for many species. Fresh mountain beech seed produced in a heavy mast year germinates readily when hand seeded into retired pasture. Shelter in the form of long grass or bracken slash is critically important to early-stage survival of beech seedlings, but release from grass competition benefits establishment (van Galen et al. 2022). Mountain beech seeds can be stored dry, vacuum-packed, and frozen at -20 °C for some years, then primed for germination via soaking and wet stratification to restore germinability (van Galen et al. 2023b). Similar storage and germination trials need to be conducted for other key native tree species, but especially other mast seeding species to ensure a continuous supply of seeds. Mast seeding species with recalcitrant seeds, such as kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub.) and rimu (*Dacrydium cupressinum* Sol. ex Lamb.), both in the southern conifer family Podocarpaceae, are especially problematic, with success dependent on using fresh seed promptly when it is available in large quantities.

The availability of appropriate soil symbionts such as mycorrhizal fungi is another component of success when seeding. In a hand-seeding trial with mountain beech, final seedling height was correlated with mycorrhizal abundance on roots (van Galen et al. 2022). Furthermore, the ability of mānuka to survive drought in another study was related to the availability of appropriate mycorrhizal inoculum (Strawsine et al. 2024). Some native trees associated with AMF fail to establish in the absence of appropriate inoculum, including conifers such as tōtara (*Podocarpus totara* G.Benn. ex D.Don, Podocarpaceae), as well as broadleaved trees, e.g. Kapuka (*Griselinia littoralis* Raoul, Griseliniaceae) (Baylis 1959; Williams et al. 2012).

Failure of seeding trials in New Zealand generally arises from poor site selection or germination, leading to low seedling survival. Seeds of many native tree species do not germinate rapidly even under optimal conditions, which places these species at a severe disadvantage in a field situation where rapid establishment before weed regrowth is desirable. Research is needed into seed priming of native species for optimal germination rates (Moss Mason 2024).

Site conditions have also been a major barrier to seeding success in New Zealand. While New Zealand has a temperate climate, some regions experience significant drought that is thought to be one of the biggest obstacles to direct drilling success nationally, especially for a flora that is not considered especially drought adapted (Douglas et al. 2007). Selection of sites with predictable rainfall, particularly in autumn and spring will likely increase the success of direct drilling for afforestation in New Zealand (Douglas et al. 2007; Streatfield 2019). The seed drilling trials mentioned in this review were mainly in areas of retired pasture, which suffered from substantial grass regrowth that often out competed slow growing native seedlings. A strict regime of repeated pre- and post-establishment herbicide applications are needed to reduce competition from weeds. Scraping away topsoil and the associated weed seed bank, and ripping to create germination microsites, are also promising avenues for further work. Seeding into relatively weed free environments after large scale weed control, such as aerial application of herbicides to invasive conifers, is another promising avenue for further research. Seeding after natural disasters (e.g., cyclones or wildfires) could also be investigated as a means for native seedlings to establish without, or with reduced, weed competition, even though wildfires were not a natural disturbance in pre-human New Zealand forests.

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CAUTION

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

8 References

Allen RB, Partridge TR, Lee WG, Efford M (1992) Ecology of *Kunzea ericoides* (A. Rich.) J Thompson (kanuka) in east Otago, New Zealand. NZ J Bot 30:135–149. https://doi.org/10.1080/0028825X.1992.10412894

Anderson SH, Ladley JJ, Robertson AW, Kelly D (2020) Effects of changes in bird community composition and species abundance on plant reproduction, through pollination and seed dispersal. Ibis 163:875–889. https://doi.org/10.1111/ibi.12938

Barber-Sperling A (2023) How far is too far? The effect of distance on the ectomycorrhizal colonisation of beech seedlings. MSc Thesis, University of Otago, Dunedin, New Zealand, 58 pp.

Baylis GTS (1959) Effect of vesicular-arbuscular mycorrhizas on growth of *Griselinia littoralis* (Cornaceae). New Phytol 58:274–280. https://doi.org/10.1111/j.1469-8137.1959.tb05358.x

Bewley JD, Black M (2013) Seeds: Physiology of Development and Germination. 2nd Edition. Springer Science & Business Media, New York, USA.

Bohoquez J, Nilsen AR, Larcombe MJ, Orlovich DA, Lord JM (2021) Spore viability and germination of some ectomycorrhizal fungi from New Zealand and implications for forest restoration. NZ J Bot 59:250–266. https://doi.org/10.1080/0028825X.2020.1862877

Brown VS, Erickson TE, Hobbs RJ, Mastrantonis S, Ritchie AL (2023) Carbon-based pelleting, soil ripping and herbicide application can be used to overcome plant recruitment barriers in Grey Stinkwood (*Jacksonia furcellata*). Ecol Manag Restor 24:119–127. https://doi.org/10.1111/emr.12583

Douglas GB, Dodd MB, Power IL (2007) Potential of direct seeding for establishing native plants into pastoral land in New Zealand. NZ J Ecol 31:143–153.

Ewers R, Kliskey A, Walker S, Rutledge D, Harding J, Didham R (2006) Past and future trajectories of forest loss in New Zealand. Biol Conserv 133:312–325. https://doi.org/10.1016/j.biocon.2006.06.018

Faulkner ME, Trotman IG, Garnet BT (1972) Aerial seeding of pines for protection afforestation; Kaweka Forest, Hawke's Bay. NZ J For 17:81–90.

Forbes AS, Wallace KJ, Buckley HL, Case BS, Clarkson BD, Norton DA (2020) Restoring mature-phase forest tree species through enrichment planting in New Zealand’s lowland landscapes. NZ J Ecol 44:1–9. https://dx.doi.org/10.20417/nzjecol.44.10

Ford M, Padamsee M, Schwendenmann L, Dopheide A, de Lange PJ (2023) The mycorrhizal communities of *Lophomyrtus bullata* Burret (Myrtaceae) within three natural forest associations of New Zealand. NZ J Ecol 47:3545. https://doi.org/10.20417/nzjecol.47.3545

Griffiths JW, Lord JM, Paull J, Pritchard ASE, Butler A, Alderton-Moss J, van der Walt K, McDonald A, Morran K (2025) Viability of seed balls for large-scale restoration of native plant communities in New Zealand. NZ J Bot *63: 1115–1131*. https://doi.org/10.1080/0028825X.2024.2432314

Heenan PB, Lee WG, McGlone MS, McCarthy JK, Mitchell CM, Larcombe MJ, Houliston GJ (2023) Ecosourcing for resilience in a changing environment. NZ J Bot 62:641–666. https://doi.org/10.1080/0028825X.2023.2210289

Helander M, Saloniemi I, Omacini M, Druille M, Salminen J-P, Saikkonen K (2018) Glyphosate decreases mycorrhizal colonisation and affects plant-soil feedback. Sci Total Environ 642:285–291. https://doi.org/10.1016/j.scitotenv.2018.05.377

Horton S, Lowther MJ, Lord JM (2024) *Anthoxanthum odoratum* (Poaceae) as a bioindicator of arbuscular mycorrhizal fungi abundance prior to native revegetation on agricultural soils. NZ J Bot *63: 2213–2223*. https://doi.org/10.1080/0028825X.2024.2409684

King CM (1990) The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

Ledgard N, Charru M, Davey H (2008) Establishing native species from seed within exotic grasslands. NZ J For 53:23–32.

Lord JM (1999) Fleshy-fruitedness in the New Zealand flora. J Biogeogr 26:1249–1253. https://doi.org/10.1046/j.1365-2699.1999.00355.x

Lord JM, Paull J, Pritchard ASE, Griffiths JW, Butler A (2025) Physical properties of seed ball formulations. NZ J Bot *63: 1715–1722*. https://doi.org/10.1080/0028825X.2025.2463505

McQueen JC, Tozer WC, Clarkson BD (2006) 19 Consequences of alien N_2-fixers on vegetation succession in New Zealand. In: Allen RB, Lee WG (eds), Biological Invasions in New Zealand. Ecol Studies Vol. 186. Springer-Verlag, Berlin, Germany, pp 295–306.

Metcalf L (2007) The Propagation of New Zealand Native Plants (2nd ed). Penguin Random House, Auckland, New Zealand.

Ministry for the Environment (2024) Projected changes to Aotearoa New Zealand’s climate. https://environment.govt.nz/facts-and-science/climate-change/climate-change-projections/climate-projections-insights-and-publications/ . (last accessed 22 November 2024).

Moss Mason KC (2024) Seeds for restoration in a changing climate: assessing seed provenancing, seed priming and seed pre-treatments in Aotearoa New Zealand. MSc Thesis, University of Otago, Dunedin, New Zealand, 202 pp.

Norton DA, Butt J, Bergin DO (2018) Upscaling restoration of native biodiversity: A New Zealand perspective. Ecol Manag Restor 19:26–35. https://doi.org/10.1111/emr.12316

Orlovich DA, Cairney JG (2004) Ectomycorrhizal fungi in New Zealand: Current perspectives and future directions. NZ J Bot 42:721–738. https://doi.org/10.1080/0028825X.2004.9512926

Otago South Rivercare (2024) Establishing natives on farm using drone technology: trial results. https://www.otagosouthrivercare.org.nz/projects_innovation/ . (last accessed 8 December 2024).

Padamsee M, Johansen RB, Stuckey SA, Williams SE, Hooker JE, Burns BR, Bellgard SE (2016) The arbuscular mycorrhizal fungi colonising roots and root nodules of New Zealand kauri *Agathis australis*. Fungal Biol 120:807–817. https://doi.org/10.1016/j.funbio.2016.01.015

Paul T, Scott M, Lennox H, Lord J (2020) Restoring wilding stands in the Wakatipu Basin by seeding native trees. Commercial report for the Wakatipu Beech Restoration Trust. Scion, Rotorua, New Zealand.

Pritchard ASE, Larcombe MJ, Steel JB, Lord JM (2024) Plant diversity under native and exotic forests: implications for transitional forestry in Aotearoa New Zealand. For Ecol Manag 572:122314. https://doi.org/10.1016/j.foreco.2024.122314

Prober SM, Byrne M, McLean EH, Steane DA, Potts BM, Vaillancourt RE, Stock WD (2015) Climate-adjusted provenancing: A strategy for climate-resilient ecological restoration. Front Ecol Evol 3:65. https://doi.org/10.3389/fevo.2015.00065

Ramana JV, Tylianakis JM, Ridgeway HJ, Dickie IA (2023) Root diameter, host specificity and arbuscular mycorrhizal fungal community composition among native and exotic plant species. New Phytol 239:301–310. https://doi.org/10.1111/nph.18911

Robertson AW, Kelly D, Ladley JJ (2011) Futile selfing in the trees *Fuchsia excorticata* (Onagraceae) and *Sophora microphylla* (Fabaceae): inbreeding depression over 11 years. Int J Plant Sci 172:191–198.

Rowarth JS, Hampton JG, Hill MJ (2007) New Zealand native seed germination requirements: A review. NZ J Bot 45:485–501. https://doi.org/10.1080/00288250709509732

Ruthrof KX, Fontaine JB, Buizer M, Matusick G, McHenry MP, Hardy GEStJ (2013) Linking restoration outcomes with mechanism: the role of site preparation, fertilisation and revegetation timing relative to soil density and water content. Plant Ecol 214:987–998. https://doi.org/10.1007/s11258-013-0224-8

Samarth, Kelly D, Turnbull MH, Jameson PE (2020) Molecular control of masting: an introduction to an epigenetic summer memory. Ann Bot 125:851–858. https://doi.org/10.1093/aob/mcaa004

Shemesh H (2024) A systematic review of nurse objects as safe sites for seedling establishment and implications for restoration. New Phytol 245:2428–2438. https://doi.org/10.1111/nph.20247

Strawsine M, van Galen L, Lord J, Larcombe M (2024) Trophic facilitation in forest restoration: can *Nothofagus* trees use ectomycorrhizal fungi of the pioneer shrub *Leptospermum*? Ecol Evol 14:e11442. https://doi.org/10.1002/ece3.11442

Streatfield S (2019) Full seed ahead: planting by machine. Department of Conservation blog. https://blog.doc.govt.nz/2019/02/15/full-seed-ahead/ (last accessed 29 July 2025)

Tan HW, Heenan PB, De Meyer SE, Willems A (2015) Diverse novel *Mesorhizobium* nodulate New Zealand native *Sophora* species. Syst Appl Microbiol 38:91–98. https://doi.org/10.1016/j.syapm.2014.11.003

Teasdale SE, Beulke AK, Guy PL, Orlovich DA (2013) Environmental barcoding of the ectomycorrhizal fungal genus *Cortinarius*. Fungal Divers 58:299–310. https://doi.org/10.1007/s13225-012-0218-1

Teste FP, Jones MD, Dickie IA (2020) Dual-mycorrhizal plants: their ecology and relevance. New Phytol 225:1835–1851. https://doi.org/10.1111/nph.16190

Van der Walt K, Kemp P, Sofkova-Bobcheva S, Burritt DJ, Nadarajan, J (2020) Seed development, germination, and storage behaviour of *Syzygium maire* (Myrtaceae), a threatened endemic New Zealand tree. NZ J Bot 59:198–216. https://doi.org/10.1080/0028825X.2020.1794911

van Galen L, Lord J, Orlovich D, Jowett T, Larcombe M (2022) Barriers to seedling establishment in grasslands: implications for *Nothofagus* forest restoration and migration. J Appl Ecol 60:291–304. https://doi.org/10.1111/1365–2664.14331

van Galen LG, Orlovich DA, Lord JM, Nilsen AR, Dutoit L, Larcombe MJ (2023a) Correlated evolution in an ectomycorrhizal host-symbiont system. New Phytol 238:1215–1229. https://doi.org/10.1111/nph.18802

van Galen L, Lord J, Orlovich D, Larcombe M (2023b) The effect of stratification and shade on germination of *Nothofagus cliffortioides* (Hook.f.) Oerst seeds. NZ J Bot 61:351–360. https://doi.org/10.1080/0028825X.2022.2156355

Veblen T, Gonzalez M, Stewart G, Kitzberger T, Brunet J (2016) Tectonic ecology of the temperate forests of South America and New Zealand. NZ J Bot 54:223–246. https://doi.org/10.1080/0028825X.2015.1130726

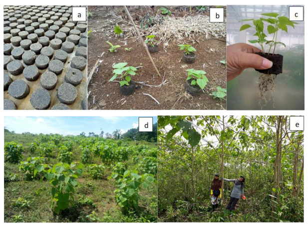
Webb CJ, Kelly D (1993) The reproductive biology of the New Zealand flora. Trends Ecol Evol 8:442–447. https://doi.org/10.1016/0169-5347(93)90007-C

Wilson DJ, Ruscoe WA, Burrows LE, McElrea LM, Choquenot D (2006) An experimental study of the impacts of understorey forest vegetation and herbivory by red deer and rodents on seedling establishment and species composition in Waitutu Forest, New Zealand. NZ J Ecol 30:191–207.

Wotton DM, McAlpine KG (2013) Predicting native plant succession through woody weeds in New Zealand. DoC Research and Development Series 336, Department of Conservation, Wellington, New Zealand.

Wyse SV, Carlin TF, Etherington TR, Faruk A, Dickie JB, Bellingham PJ (2024) Can seed banking assist in conserving the highly endemic New Zealand indigenous flora? Pac Conserv Biol 30:PC23029. https://doi.org/10.1071/PC23029

Xiao X, Wei X, Liu Y, Ouyang X, Li Q, Ning J (2015) Aerial seeding: an effective forest restoration method in highly degraded forest landscapes of sub-tropic regions. Forests 6:1748–1762. https://doi.org/10.3390/f6061748



Seeding of tropical tree species in Indonesia

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Abstract

Indonesia's more than 120 million ha of forest are considered a global biodiversity hotspot. Over-exploitation, land conversion, fires, and natural disasters have degraded almost 13 million ha. In response, the government has launched various restoration programs, aiming to reduce greenhouse gas emissions and decrease vulnerability to disasters like floods, landslides, and droughts. Indonesia aims to restore 12 million ha of forests and 2 million ha of peatlands by 2030. Seeding is a cost-effective alternative to planting seedlings, suitable for large-scale restoration, especially in remote or labor-limited areas. Success depends on species selection, seed quality, land preparation, timing, and maintenance. Seed encapsulation in briquettes or balls can be adapted for aerial seeding using drones or helicopters. Biofertilizers and hydrogels can improve germination and survival. Medium- to large-seeded species generally perform better in seeding applications. Land preparation (clearing and soil loosening at the sowing point or plot) and optimal sowing time (early-mid rainy season) are critical for success. Weeds are controlled around seedlings typically for up to three years until plants are established. Seeding costs about half as much as planting polybag seedlings for the same number of surviving plants. Further research is needed to optimize seeding practices for various species and site conditions.

Keywords

tropical rain forest, seed traits, seed briquettes, biofertilizer, aerial seeding, cost comparison

Contents

1 The Indonesian forest

Indonesia is a tropical country with a large forest area of about 120.47 million ha (MoEF 2022), or around 64% of the total land base of the country. Most forests in Indonesia are categorized as evergreen tropical rainforests that grow wherever rainfall exceeds evapotranspiration (annual rainfall is more than 2,000 mm). The dry season is no longer than 2 months (Elliott et al. 2013). These forest areas are managed based on their function, i.e., production forests (68.8 million ha), protection forests (29.6 million ha), conservation forests (22.1 million ha), and additionally forests associated with marine conservation areas (5.3 million ha) (MoEF 2020). Indonesian forests are one of the significant forest areas recognized for maintaining global climate balance, including the Amazon forests in South America and tropical forests of the Congo Basin in Africa, and are popularly known as the lungs of the world. Indonesia has more than 17,000 islands, which makes Indonesian forests one of the greatest reservoirs of biodiversity after Brazil and Colombia and is included as a "Global Biodiversity Hotspot" (Butler 2016). A total of 1605 bird species, 720 mammal species, 723 reptile species, 5137 arthropod (spider) species, 248 freshwater fish species, 15,1847 insect species, and 197,964 invertebrate species have been documented as living in Indonesian forests. Indonesian forests also grow 120 species of gymnosperms and an estimated 30,000 to 40,000 species of angiosperms, and to date, only 19,112 plants species have been identified (MoEF 2020a).

Over-exploitation, forest encroachment, land conversion, forest fires, and the impact of natural disasters have increased forest and land degradation (MoEF 2024). The existence of degraded forests and lands often trigger forest fires, the release of large amounts of greenhouse gases, changes in microclimate and weather patterns (Ayres and Lombardero 2000, CIFOR 2013), and increased vulnerability to disasters, especially hydrometeorological disasters (BNPB 2016). To overcome forest destruction, the Indonesian government has attempted to reduce the area of degraded forests and landscapes through various restoration programs such as Social Forestry (2002), the National Movement for Forest and Land Rehabilitation (2003), the construction of 57 permanent nurseries (2011), the KPH (Forest Management Unit) nursery (2015), community nurseries (2016), village nurseries (2020), and the construction of six nursery centers (2021) to provide seedlings on a large scale. However, according to data from the Ministry of Environment and Forestry (MoEF 2022), the area of degraded forest and land in Indonesia is still large, i.e., 12.74 million ha, consisting of 8.70 million ha categorized as critical and 4.04 million ha designated as very critical. The parameters determining critical and very critical land are based on Forestry Ministerial Regulation Number P.32/Menhut-II/2009, including land cover, slope gradient, erosion hazard level, and management. Each parameter determining critical land is given a specific score (land cover, slope gradient, and management ranges from 1 to 5; erosion ranges from 2 to 5) and weighting (land cover = 50%, slope gradient = 20%, erosion = 20%, and management = 10%). The sum of each score is then classified to determine the level of critical land. Based on these calculations, the level of land criticality is classified into 5 classes, i.e., very critical (score 120-180), critical (score 181-270), somewhat critical (score 271-360), potentially critical (score 361-450), and not critical (score 450-500).

Forest degradation and deforestation are major factors affecting biodiversity decline and climate change (MoEF 2024). Forests and lands that have been degraded and identified as critical are generally overgrown with brush, reeds, and grasses (Order Poales), have low fertility, and are prone to erosion. Meanwhile, severely degraded land (very critical land) is often grassland or barren land that is severely eroded (gully erosion) with loss of soil, including the entire A horizon and part of the B horizon (Wahyunto and Dariah 2014). Increasing temperatures and shifting rainfall patterns are increasing the area of land noted as critically degraded because of their impacts on ecological, hydrological, and production functions (MoEF 2024). This crisis has encouraged the Indonesian government to prioritize land and forest restoration activities.

Through the Nationally Determined Contribution (NDC) program as a commitment to the United Nations Framework Convention on Climate Change (UNFCCC), the Government of Indonesia (GoI) plans to restore 12 million ha of forests and 2 million ha of peatlands by 2030 (MoEF 2021). The GoI has also set a target for restoring 600,000 ha of degraded mangrove (*Avicennia* spp. L.) forests (Murdiyarso and Ambo-Rappe 2022). As part of the implementation of the NDC, the GoI through the National Program "Indonesia's FOLU Net Sink 2030" as stipulated in Presidential Regulation Number 98 of 2021, targets to achieve net zero emissions in the forestry and land sector by 2030. The success of this forest and landscape restoration (FLR) program will determine whether these targets are achieved. Apart from that, FLR will also contribute to meeting other governmental commitments to sustainable development goals (SDGs), the Paris Agreement on Climate Change, Aichi Biodiversity Targets, Control of Land Degradation (UNCCD), and various other international conventions.

2 Impacts of deforestation and forest degradation

Massive exploitation of the natural forest in Indonesia began in 1975 with the issuance of Forest Tenure Rights (HPH) permits that aimed to increase state income and human welfare (Nawir et al. 2017). Apart from that, forest areas have also experienced pressure due to widespread land conversion to crop estates, settlements, and other non-forestry interests (Frastien 2017; Juniyanti et al. 2021). These licensing policies are often not balanced with an optimal monitoring and control system, increasing the area of degraded forests and lands. In 2000, the area of degraded forests and lands in Indonesia was estimated at around 23.2 million ha, and this continued to increase until 2007 to 77.8 million ha. With intensive forest landscape restoration (FLR) efforts, the area of forest and degraded land had declined to about 14 million ha in 2020 (MoEF 2020b). In 2022, the area of degraded forests and land remained around 12.77 million ha (MoEF 2022).

Deforestation and degradation release large amounts of greenhouse gases (GHG) that contribute to climate change (Hansen et al. 2001). In turn, global climate change influences regional and local climate conditions that impact weather patterns (Ayres and Lombardero 2000; CIFOR 2013). Tropical forests such as those in Indonesia are carbon sinks that help to mitigate climate change. However, forest destruction, conversion to other land uses, and escaped agricultural fires once caused Indonesia to be the third-largest emitting country in the world. Of the GHG emissions produced by

Indonesia, 85% comes from deforestation and peatland conversion (Wijaya et al. 2017). In 2015 and 2016, fires in the forestry and peat sectors contributed 66% and 43% of emissions (BPS 2019).

The existence of degraded forests and land has also increased the vulnerability of several regions in Indonesia to various natural disasters, such as floods, landslides, and droughts, which cause loss of life and extremely high property losses. According to the Indonesian Disaster Information Data (DIBI)-BNPB, of the more than 1,800 disaster events in the period 2005 to 2015, more than 78% (11,648) were hydrometeorological disasters, and only around 22% (3,810) were geological disasters. Hydrometeorological disasters include extreme weather (cyclones and tropical storms), extreme ocean waves, floods, drought, and land and forest wildfires. The incidence of these disasters is tending to increase (BNPB 2016). Geological hazards include tsunamis, landslides, and volcanic activities. The severity of most disasters, such as floods, landslides, droughts, and tsunamis, are closely related to land cover conditions (FAO 2005; Maginnis and Elliott 2005). For example, because forests can increase infiltration and reduce runoff, they reduce the threat or severity of floods, droughts, and other hydrometeorological disasters (FAO 2005; Bonell and Bruijnzeel 2005). Forested areas tend to be more resistant to landslides (Schmaltz et al. 2017), and mangrove forests provide physical protection during extreme wave and tsunami events (Maginnis and Elliot 2005).

Deforestation and forest degradation have also threatened the biodiversity of flora and fauna in Indonesia (Budiharta et al. 2011). IUCN Red List data (2021) show that 1 Indonesian tree species is Extinct, 3 species are Extinct in the Wild, and 856 species are threatened with extinction (170 Critically Endangered, 279 Endangered, and 407 Vulnerable tree species). Threats to several species of flora and fauna are caused by over-exploitation and habitat loss. Many of these threatened species could be sustainably used by humans if effective and comprehensive conservation efforts were established to ensure species viability.

3 Initiating seeding in Indonesia

FLR is one means of mitigating climate change and reducing the area of deforested and degraded forests. Conventional seedling planting programs have been used to reduce the area of deforested and degraded land. In 2020, the area that could be planted through the FLR program of the Ministry of Environment and Forestry was estimated at 207,650 ha (MoEF 2020b), so if all currently planned efforts are carried out, it will require many years to restore this area of degraded forest. For this reason, alternative methods capable of quickly afforesting/reforesting land on a large scale are needed; seeding is one such alternative (Sudrajat et al. 2023).

Seeding is a long-standing forestation practice being considered for FLR because of its relatively lower cost and labor requirements compared to conventional seedling planting (Sudrajat et al. 2018; Louhaichi et al. 2021; Downer et al. 2024; Sudrajat et al. 2024). Though potentially useful, this technique is often less dependable than planting seedlings (Brown and Lugo 1990). Several obstacles to its application include competition from surrounding plants (weeds) (Holl 1998; Nurhasybi and Sudrajat 2009), lack of precise microsite conditions for germination (Doust et al. 2006), and occurrence of seed predators and seedling herbivores (Holl et al. 2000; Nurhasybi and Sudrajat 2013). Weather conditions also play a significant role in determining the success of seeding (Sudrajat et al. 2023). Apart from these general obstacles, selecting species suitable for seeding on particular sites has not yet been widely determined (Figueiredo et al. 2021; Naruangsri et al. 2024). Further study is necessary to identify the characteristics of tropical forest tree species that are suitable for seeding (Doust et al. 2008; Naruangsri et al. 2024).

4 Seed procurement and preparation

4.1 Species selection

Species vary in suitability for seeding applications; generally, species with medium- to large-sized seeds show better seedling establishment. They have large nutrient reserves, resulting in better germination and more vigorous seedlings (Hossain et al. 2014; Ceccon et al. 2016; De Sousa and Engel 2018). In addition, suitable species must produce seedlings that grow quickly, fast enough to compete with weeds early in their development. In general, pioneer species have faster initial growth, but species with very small seed (e.g., *Neolamarckia* spp. Bosser and *Eucalyptus* spp. L'Hér.), that require a more open site to germinate, have early seedling growth that is very susceptible to biotic and abiotic stress (Camargo et al. 2002). Several tropical trees have the potential to be used in seeding, such as *Anacardium occidentale* L., *Calophyllum inophyllum* L., *Gmelina arborea* Roxb., *Acacia* spp. Mill., *Enterolobium cyclocarpum* (Jacq.) Griseb., and *Intsia bijuga* (Colebr.) Kuntze among other species (Engel and Parrotta 2001; Hobert et al. 2020).

Apart from the need for species to be suited to seeding, the seeds used must be of good quality. Results of trials on 24 tropical tree species show that large (heavy) seeds tend to produce higher seedling survival. Likewise, seeds with high germination capacity (laboratory test results) show a positive correlation with seedling survival in the field (Figure 1).

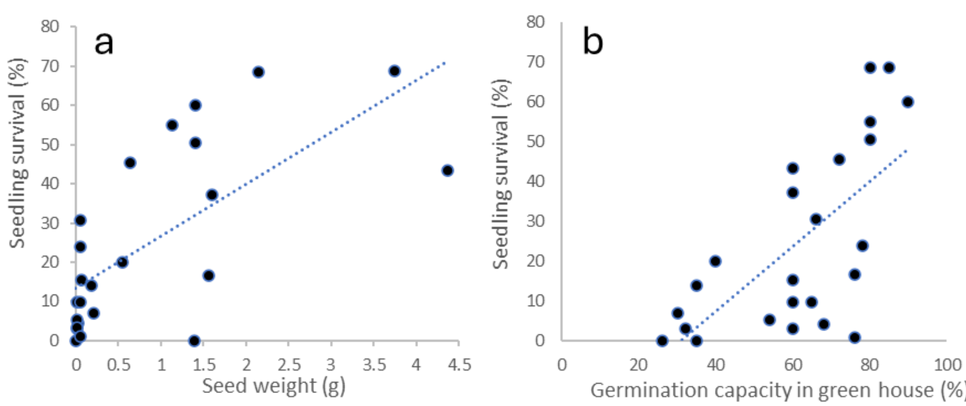

Figure 1. Correlation trends between seedling survival at 12 months and seed traits for some tropical trees: a) seed weight, b) germination capacity.

4.2 Delivery systems

Different delivery systems have been developed to improve the success of seeding. Encapsulating seeds in rooting media, often supplemented with nutrients, protectants, and inoculants, singly or in combination, have been developed. The method was developed in Scandinavia in the 1930s (Heiberg 1934) using forest soil or peat and paraffin. Fukuoka (1973) described the use of seed balls, which are a mixture of seeds, soil, water, and clay. Seed balls contain a basic unit of media for plant growth and can provide the ingredients plants need for unique site situations. Clay, which is a mixing medium, also functions to reduce water loss by increasing water potential and reducing seed predation. Seed pellets or briquettes can be placed on the soil surface or planted in the soil (Sudrajat et al. 2018); seed balls have been adapted for delivery by drone (Stanturf et al. 2024).

Using seed briquettes or seed pellets can increase seeding success by reducing risks (Sudrajat et al. 2018; Nuhasybi and Sudrajat 2018; Sudrajat et al. 2023). Apart from protecting seeds from seed predators, seed briquettes also function as a delivery system for biological and chemical treatments to increase seed germination and seedling growth (Taylor et al. 2004; Gevrek et al. 2012; Sudrajat et al. 2023). For example, seed briquettes increased the germination of *Lycopersicon esculentum* Mill. seed, and the effect was like a priming treatment (Govinden-Soulange and Levantard 2008). The use of seed briquettes for seeding is also thought to improve biological control capacity (Choong et al. 2006), increase germination capacity and speed (Podlaski and Wyszkowska 2003; Tamilarasan et al. 2021), and increase resistance to drought stress (Abusuwar and Eldin 2013; Sudrajat et al. 2023).

Seed briquettes can be used with orthodox and intermediate recalcitrant seeds. For orthodox seed, a briquette can be made with 20% soil, 40% compost, 25% rice (*Oryza sativa* L.) husk charcoal, 10% lime, 5% tapioca, and 2 g mycorrhiza inoculum. For intermediate seed, a slightly different mixture is used: 10% soil, 40% compost, 30% rice husk charcoal, 15% lime, 5% tapioca, and 2 g mycorrhiza (Sudrajat and Rustam 2020). Briquette size must be adjusted to the size of the seed. Small seeds will have difficulty germinating in a large briquette. For small seeds, such as *Acacia* spp. and *Calliandra* spp. Benth., briquettes that are 2-3 cm in diameter are best, particularly round or flat briquettes (Sudrajat et al. 2019). In contrast, for *G. arborea*, a round, flat briquette of 5 cm diameter and 3 cm thickness is quite effective in increasing germination and growth of seedlings when sown directly in the field (Sudrajat and Rustam 2020).

4.3 Biofertilizer application

The addition of mycorrhizae to seed briquettes can improve seedling survival through the first month of growth (Sudrajat and Rustam 2020). Mycorrhizae tend to increase plant growth (Bayozen and Yildiz 2009), favorably change the biochemical composition of cells (Jaiti et al. 2008; Neeraj and Singh 2011), and reduce incidence of plant disease (Zachee et al. 2008; Neeraj et al. 2011). Mycorrhizae may also increase plant resistance to drought stress (Manoharan et al. 2010). Dark septate endophytes (DSE) are another biofertilizer that can improve seedling survival and growth (Widyani et al. 2024). Inoculations of mycorrhizae and DSE can increase absorption of water and nutrients, support disease prevention, and remove toxic metals from soil (Brady and Weil 1999; Widyani et al. 2024).

Seeding trials using briquettes with the addition of arbuscular mycorrhizal fungi (AMF) and DSE resulted in a better survival rate of *Ceiba pentandra* (L.) Gaertn. and *Leucaena leucocephala* (Lam.) de Wit 12 months after sowing. In *C. pentandra*, AMF and DSE inoculations had a significant effect on the percentage of colonization, while in *L. leucocephala*, inoculation had no significant effect on the percentage of AMF and DSE colonization. Most seeds and seed briquettes infected with AMF and DSE had higher seedling survival than the control (Widyani et al. 2024).

5 Land preparation

Land preparation that provides an optimal germination environment for seeding typically improves success. Land preparation involves creating a strip cleared of undergrowth and bushes 80-100 cm wide to facilitate sowing. On this strip, plots are made for sowing seeds or seed briquettes cleared of grass and other vegetation with a 40-50 cm radius to provide optimal germination conditions. Site (plot) clearing with burial of large seed briquettes (diameter 5 cm) in soil gave better seedling survival for *G. arborea* (57%) than for medium-sized seed briquettes with a diameter 3 cm (38%) or small seed briquettes with a diameter 2 cm (29%) briquettes; burial, however, did not improve germination and seedling survival for seed sown in medium or small briquettes. Similarly, for *E. cyclocarpum*, seed briquettes buried on cleared land gave the best germination and survival (52.5%), while those sown on unprepared sites showed germination and survival of only 3.7%. Additionally, land prepared with clearing and soil loosening provided the best height growth (Sudrajat et al. 2019).

6 Plant establishment

6.1 Sowing season

The success of plant establishment with seeding is largely determined by the sowing time. Determining the right time to sow seed can affect the survival and growth of seedlings such as *Acacia pycnantha* Benth., *A. acinacea* Lindl., and *Eucalyptus microcarpa* (Maiden) Maiden (Carr at el. 2007). For example, seeding briquettes of several tropical tree species that were sown on four dates in the Parung Panjang Forest Area in Bogor showed the best results for an early-mid rainy season sowing (mid-December). At that time, the frequency of rain had stabilized, which is important because sowing at the beginning or before the rainy season adds risk of drought if the rain stops for 1 to 3 weeks. Likewise, sowing toward the end of the rainy season resulted in high mortality due to the lack of daily rainfall (Sudrajat et al. 2023). The best germination and seedling survival of C. *pentandra, E. cyclocarpum*, and *C. inophyllum* were respectively, 23.9%, 55.0%, and 68.7% in December for seed encapsulated in briquettes and treated with Aquasorb, compared to briquettes or Aquasorb alone (Sudrajat et al. 2023). Aquasorb is a hydrogel or hydrophilic polymer that can absorb and store water up to hundreds of times its weight when it rains and slowly release it when the surrounding soil dries, thus improving germination and early growth of seedlings by reducing effects of drought (Tongo et al. 2014).

6.2 Sowing techniques

Sowing seed or seed briquettes on the surface of the soil is quite efficient and saves labor, but there is a risk that the seed will be washed away by rainwater or predated by animals. According to Johnson (1980), seeding depth will affect germination capacity. Seeding depth must be adjusted to the size of the seed. For example, the best germination of *I. bijuga*, which has a seed length and width of around 2-3 cm, was observed for seeds buried 3 cm deep (Nurhasybi and Sudrajat 2009);

likewise, seed briquettes (with a thickness of 3 cm) supported best germination when buried 3 cm deep (Sudrajat et al. 2018). Seed sowing is generally done manually using a hoe to make placing the seeds or seed briquettes easier. The number of seeds sown per ha is adjusted to the quality of the seeds (results of laboratory germination tests) and the adaptation of the species. For *Swietenia macrophylla* King, with a germination test result of 80%, the target of 1000 plants per ha in the first year is achieved by sowing 1,838 seed briquettes, or 3,906 seed without briquettes (Sudrajat et al. 2024). For *C. inophyllum* with a germination rate of 80%, the target of 1000 plants in the first year is achieved by sowing 1,613 seed briquettes or 5,000 seeds (Sudrajat et al. 2018). Using mixed species can reduce the risk of failure due to attacks by seed and seedling predators and increase biodiversity.

Aerial seeding using helicopters or drones has been conducted at large and remote areas in Indonesia (Andrio 2018). Helicopters were used in several remote areas of Indonesia, such as South Kalimantan, South Sulawesi, and West Java. Drones are being tested for aerial seeding applications to restore degraded mangrove forests—3 cm diameter seed balls of *Avicennia* spp. coated with a biofertilizer are being used in these tests. The drone can sow 600 seeds in 20 minutes from an altitude of 5 m. Given a 1 m x 2 m sowing spacing, one drone can sow 3 ha day^{-1}. As a complement to conventional community-based mangrove planting, this drone technology is suitable for establishing mangroves in areas that are difficult to access, sparsely populated, and remote (Syukra 2021).

7 Post-sowing practices and maintenance

Maintenance of seeded stands is conducted in a minimalist manner, i.e., controlling weeds around seedlings to provide space for growth and free the plants from vining weeds. Weed control is done manually with a machete or other tools by freeing plants from weeds in a radius of 0.5 m around the plant. Weeding is done twice yearly, at the beginning of seedling growth, until the plant is vigorous enough to compete with weeds. Weed control continues for fast-growing trees, typically for three years.

8 Successful seeding

8.1 Seedling survival and growth

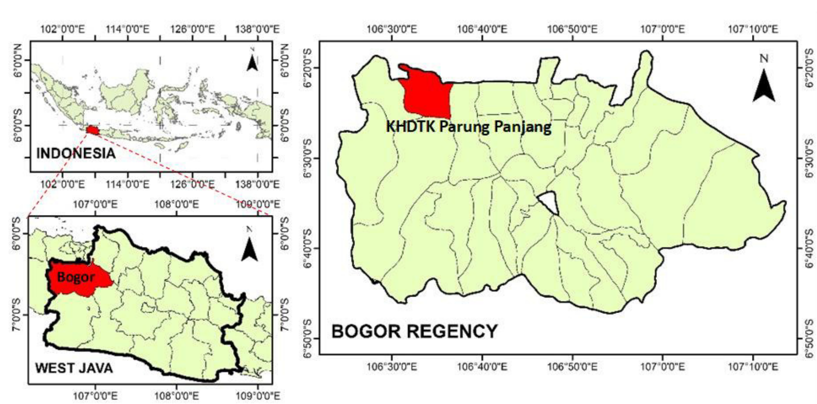

Figure 2. Seeding trial location in Parung Panjang Forest Area (KHDTK Parung Panjang) in Bogor, Indonesia.

Seeding of 24 tropical tree species using seed briquettes in the Parung Panjang Forest Area, Bogor, West Java (Figure 2) showed five species with high germination and first-year seedling survival (>50%) (Figure 3). The species with high survival were *S. macrophylla, C. inophyllum, E. cyclocarpum, Pongamia pinnata* (L.) Pierre, and *Hymenaea verrucosa* Gaertn. (Figure 3). Seedling survival was correlated with seed weight, length, width, and initial germination capacity (r^2 = 0.686, 0.729, 0.762, and 0.670, respectively). Sowing seeds encapsulated in briquettes increased seedling stem diameter compared to sowing unencapsulated seeds.

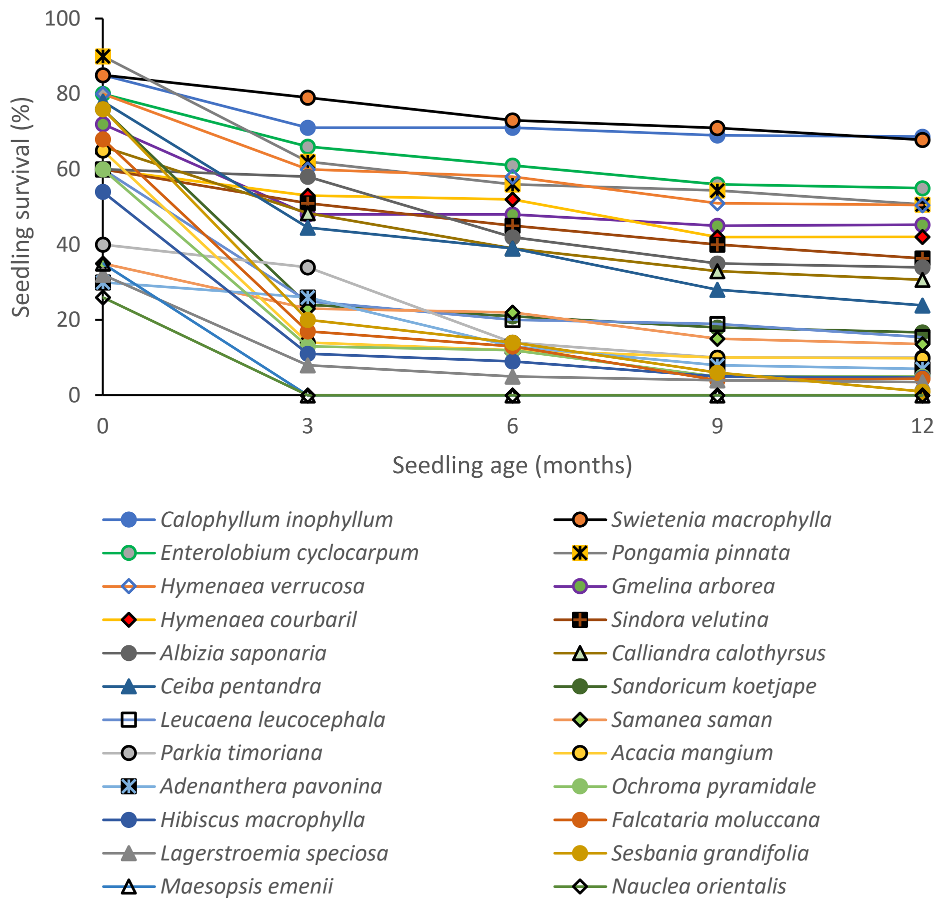

Figure 3. Percentage of normal seedlings based on the germination test (0 month) and seedling survival of seeded trees in the Parung Panjang Forest Area, Bogor, West Java (3, 6, and 12 months) (Sudrajat et al. 2021). Seed were treated prior to the germination test and prior to seeding as follows. 1) Seeds treated by soaking in hot water (80 °C) and letting them cool for 24 hours (*Acacia mangium* Willd., *Adenanthera pavonine* L., *Albizia saponaria* (Lour.) Blume ex Miq., *Calliandra calothyrsus* Meisn.*, Enterolobium cyclocarpum* (Jacq.) Griseb.*, Falcataria moluccana* (Mic.) Barneby & J.W. Grimes*, Leucaena leucocephala* (Lam.) de Wit, *Parkia timoriana* (DC.) Merr., *Samanea saman* (Jacq.) Merr., and *Sesbania grandifolia* (L.) Poir.). 2) Seeds treated by stripping the exodermis (*Calophyllum inophyllum* L.). 3) Seeds treated by soaking in water for 24 hours (*Ceiba pentandra* (L.) Gaertn., *Gmelina arborea* Roxb., *Lagerstroemia speciosa* (L.) Pers., and *Ochroma pyramidale* (Cav. ex Lam.) Urb.). 4) Seed treated by soaking in H_2SO_4 for 20 minutes (*Hibiscus macrophyllus* Roxb. ex Hornem.*, Hymenaea courbaril* L., *Hymenaea verrucosa* Gaertn.*, Maesopsis emenii* Engl.*,* and *Sindara velutina* Baker). 5) Seed treated by hydrating in wet straw paper for 24 hours (*Pongamia pinnata* (L.) Pierre, *Sandoricum koetjape* (Burm.f.) Merr., and *Swietenia macrophylla* King). 6) Seed that was not treated (*Nauclea orientalis* (L.) L.) (Sudrajat et al. 2017).

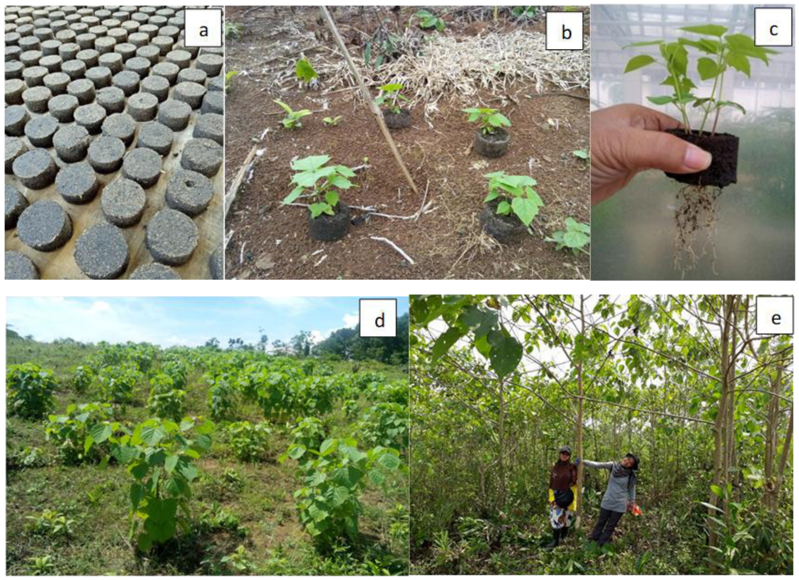

Figure 4. Seeding of *Gmelina arborea* Roxb. encapsulated in seed briquettes: a) seed briquettes, b, c) germinated *G. arborea* in seed briquettes, d) 1-year-old seedlings, e) 2.5-year-old trees (Photo credits: Dede Sudrajat).

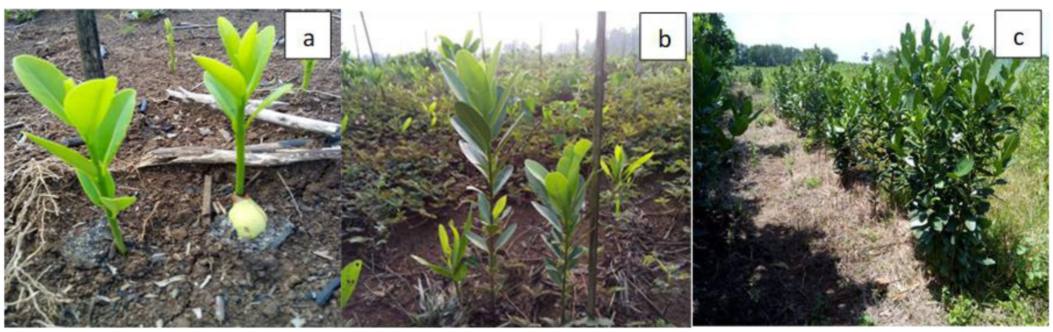

Figure 5. Seeding of *Calophyllum inophyllum* L. using seed briquettes: a) 2-month-old seedlings, b) 6-month-old seedlings, c) 2-year-old saplings. (Photo credits: Dede Sudrajat).

A comparative growth study of plant establishment methods with *C. inophyllum* examined seeding, seeding using seed briquettes, bareroot seedlings, polybag seedlings, and bio-pot seedlings. Bio-pots molded from an organic medium (a mixture of compost (40%), soil (20%), rice husk charcoal (20%), lime (10%), and tapioca (10%) as an adhesive) are used to grow seedlings in a nursery (Sudrajat et al. 2018). Polybag and bio-pot seedlings had the best survival and growth in height and diameter, while seeding without briquettes showed the lowest germination, survival, and growth (Table 1). Sowing seed in briquettes resulted in plants with the longest tap root, tap roots of greatest mass, and the highest overall root dry weight (Figure 6) (Sudrajat et al. 2018).

On the one hand, trees established through conventional seedling planting are more uniform, able to tolerate or avoid environmental or biological stress, and can reach maturity quicker than those established through seeding (Liptay et al. 1982). Sown seed is subject to poor germination and new germinants typically show slower, have more variable growth, and are more susceptible to extreme temperatures, drought stress, heavy rains, or pests and diseases than are planted seedlings (Heydecker and Coolbear 1977). On the other hand, sowing seed in briquettes tends to produce plants with a more balanced root system, a longer tap root, and a greater total root dry weight. The shoot-root ratio of seedlings originating from seeding is 3.8, which is more balanced than the shoot-root ratio of polybag seedlings (4.5) (Sudrajat et al. 2018). Seedlings produced from seeding develop a natural root system that is structured for the prevailing site conditions. Seedlings grown in polybags, common in the tropics, often are stunted or deformed (Tsakaldimi et al. 2009; Haase et al. 2021) and vulnerable to drought (Canadell et al. 1996).

Table 1. Comparison of *Calophyllum inophyllum* L. seedling survival, height, and root collar diameter relative to several plant establishment methods (Sudrajat et al. 2018).

Method	Seedling survival (mean ± SD)[1] (%)	Height (mean ± SD) (cm)	Root collar diameter (mean ± SD) (mm)
Seeding	20 ± 5 d	25.86 ± 9.06 c	4.38 ± 1.54 c
Seeding with briquettes	61 ± 5 c	32.77 ± 0.69 b	6.14 ± 2.10 bc
Bareroot seedling	84 ± 4 b	37.38 ± 9.63 b	6.34 ± 1.43 b
Polybag seedling	98 ± 2 a	46.15 ± 5.40 a	7.79 ± 2.62 ab
Blocked media seedling	98 ± 1 a	48.12 ± 7.85 a	9.26 ± 1.11 a

[1] Different letters in a column denote statistical difference ($P \leq 0.05$) between treatments.

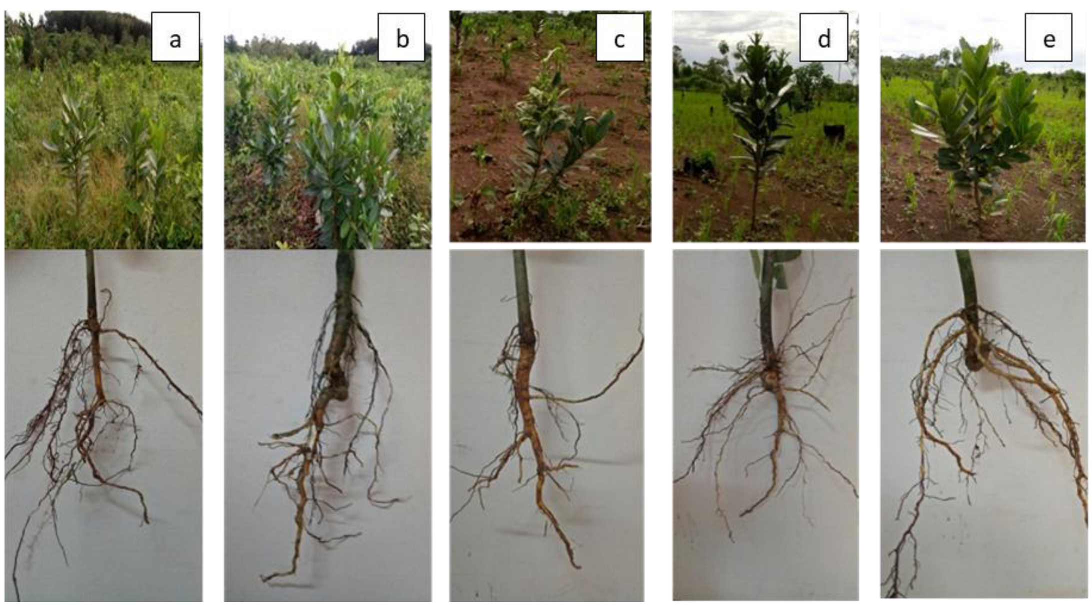

Figure 6. Comparison of growth and root form of 5 plant establishment methods for *Calophyllum inophyllum* L., a) seeding, b) seeding with briquettes, c) bare-root seedlings, d) polybag seedlings, and e) blocked media seedling. (Photo credits: Dede Sudrajat 2018).

8.2 Seedling establishment cost comparison

The costs of producing and establishing trees vary greatly depending on many factors including the materials used in production, size of the target plant, establishment method, survival in the field, and other factors such as transportation and labor. A comparison of plant production costs based on 1000 target plants indicates that seeding is generally the least expensive establishment alternative (Sudrajat et al. 2018; Sudrajat et al. 2024). Cole et al. (2011) reported a similar finding: planting seedlings typically cost 2 to 4 times more than seeding depending on the level of maintenance provided.

One of the biggest uncertainties in calculating the cost of seeding, however, is the percentage germination and survival assumptions, because this depends on the season of sowing, microclimate, seed viability, and other factors. Nevertheless, use of seed encapsulated in briquettes was about half the cost of planting bio-pot or polybag seedlings (based on the calculations in Table 2). Assuming 1000 surviving *C. inophyllum* seedlings at 9 months, seeding with seed encapsulated in briquettes provided the lowest cost (USD 199.80 = IDR 3,167,815), followed by seeding without briquettes, then planting bareroot seedlings (Sudrajat et al. 2018). Establishing seedlings raised in bio-pots had the highest cost, slightly more than seedlings raised in polybags (Table 2).

Table 2. Comparison of establishment costs for *Calophyllum inophyllum* L. plants using seeding, seeding with briquettes, bareroot seedlings, polybag seedlings, or bio-pot seedlings weighted for 1000 surviving seedlings at the Parung Panjang Forest Area, Bogor (Sudrajat et al. 2018).

Item	Seeding		Seeding with briquette		Bareroot seedling		Polybag seedling		Blocked media seedling	
	Unit	Cost (IDR)	Unit	Cost (IDR)	Unit	Cost (IDR)	Unit	Cost (IDR)	Unit	Cost (IDR)
Seed cost [1]	5000	50000	1613	16130	1429	14290	1224	12240	1224	12240
Seed pellet production [2]			1613	233885						
Seedling production [3]					1190	466480	1020	624240	1020	770100
Transportation [4]	5000	50000	1613	50000	1190	100000	1020	400000	1020	400000
Land preparation [5]	1 ha	2706500	1 ha	2706500	1 ha	2706500	1 ha	3721400	1 ha	3721400
Sowing cost [6]	5000	500000	1613	161300						
Planting preparation [7]					1000	500000	1000	500000	1000	500000
Digging planting holes cost [8]					1000	300000	1000	500000	1000	500000
Planting cost [9]					1000	100000	1000	200000	1000	200000
Total (IRD)		3,306,500		3,167,815		4,172,980		5,946,864		6,091,500
Total (USD)		209		200		263		375		384

Notes: [1] *C. inophyllum* seed price IDR 3,000 kg^{-1}, germination capacity 80%, seedling survival for each method based on Table 1; [2] Production cost per pellet; [3] Production cost bareroot, polybag, and blocked media seedlings; [4] Pickup charge for blocked media and polybag seedlings and courier charge for seed/seed pellet; [5] Based on standard of Ministry of Forestry, Republic of Indonesia No. P.64/Menhut-II/2009 (Standard biaya pembuatan hutan tanaman industri dan hutan tanaman rakyat), range of land preparation cost IDR 2,706,500-3,721,438; [6] Sowing cost IDR 100 per seed/seed pellet; [7] Planting preparation (making and setting up planting marker/stake in the field) for 1000 seedlings and IDR 500 per stake, seedling stock was prepared for replanting; [8, 9] Planting hole digging and planting cost based on experience of work performance per worker in Parung Panjang, Bogor, IDR 500 per a planting hole, IDR 200 per planting of a seedling; currency in 2018: 1 USD = IDR 15,854

9 Conclusion

Seeding is an alternative afforestation/reforestation method that holds promise for cost effective forest restoration in Indonesia, particularly considering the amount of land designated by the Indonesian government as critical or very critical for FLR. Opportunities to employ seeding practices for forest restoration are most obvious in remote areas, areas with limited access, and regions where funding or labor availability are in short supply. However, there are drawbacks to seeding that can compromise restoration success. Failures are often caused by poor planning and inattentive implementation that does not fully consider the environmental conditions of the restoration site or best technical procedures. Initial research in Indonesia indicates that seeding success can be increased through attention to several factors—these include selecting appropriate species (easily germinating, adapted to critical land, and early competitiveness with weeds), land preparation (soil conditioning to support germination and early seedling growth), use of quality seed (high viability), encapsulating seed in briquettes or balls, application of biofertilizers and hydrogels (mycorrhiza, DSE, aquasorb, and others), sowing at the appropriate time, and plantation maintenance (weed control around established seedlings). Too, the efficiency of seeding operations can be improved with aerial seeding technology (helicopters or drones) in certain situations such as for mangrove forests. Advancing seeding as a conventional forest restoration practice in Indonesia will require additional research broadened to include many important plant species, various site conditions, seeding technologies, and other key factors that impact success.

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This paper may include research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All use of pesticides must be registered by appropriate agencies before they can be recommended.

CAUTION

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

11 References

Abusuwar AO, Eldin AK (2013) Effect of seed pelleting and water regime on the performance of some forage species under arid conditions. American-Eurasian J Agric Environ Sci 13(5):728-734. https://doi.org/10.5829/idosi.aejaes.2013.13.05.1961

Andrio A (2021) Development of UAV technology in seed dropping for aerial revegetation practices in Indonesia. IOP Conference Series: Earth and Environ Sci 308:012051. https://doi.org/10.1088/1755-1315/308/1/012051

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286. https://doi.org/10.1016/S0048-9697(00)00528-3

Bayozen A, Yildiz A (2009) Determination of mycorrhizae interactions and pathogenicity of *Rhizoctonia solani* Kuhn isolated from strawberry and *Xanthium strumarium*. Turk J Biol 33:53-57. https://doi.org/10.3906/biy-0801-15

Birkedal M, Löf M, Olsson E, Bergsten U (2010) Effects of granivorous rodents on direct seeding of oak and beech in relation to site preparation and sowing date. For Ecol Manag 259:2382-2389. https://doi.org/10.1016/j.foreco.2010.03.014

BNPB (Badan Nasional Penanggulangan Bencana) (2016) Resiko Bencana Indonesia. Badan Nasional Penanggulangan Bencana. Jakarta, Indonesia.

Bonell M, Bruijnzeel LA (2005) Forests, water and people in the humid tropics: past, present and future hydrological research for integrated land and water management. Cambridge University Press, Cambridge, UK.

BPS (Badan Pusat Statistik) (2019) Statistik Lingkungan Hidup 2019 (Environment Statistics of Indonesia 2019). Badan Pusat Statistik. Jakarta, Indonesia.

Brady NC, Weil RR (1999) The nature and properties of soils. 12th Edition, Prentice-Hall, Publishers, London, UK.

Budiharta S, Widyatmoko D, Irawati, Wiriadinata H, Rugayah, Partomihardjo T, Ismail, Ugi T, Keim AP, Wilson K (2011) The processes that threaten Indonesian plants. Oryx 45:172-179. https://doi.org/10.1017/S0030605310001092

Butler RA (2016) The top 10 most biodiverse countries. Mongabay. https://news.mongabay.com/2016/05/top-10-biodiverse-countries (last accessed 13 Dec. 2024).

Camargo JLC, Ferraz DK, Imakawa AM (2002) Rehabilitation of degraded areas of Central Amazonia using direct sowing of forest tree species. Restor Ecol 10(4):636–644. https://doi.org/10.1046/j.1526-100X.2002.01044.x

Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583-595.

Carr D, Bonney N, Millsom D (2007) The effect of sowing season on the reliability of direct seeding. Rural Industries Research and Development Corporation, Publication No. 07/105 Project No. GAL-6A, Kingston, Australia.

Ceccon E, González EJ, Martorelli C (2016) Is direct seeding a biologically viable strategy for restoring forest ecosystems? Evidence from a meta-analysis. Land Degrad Dev 27(03):511-520. https://doi.org/10.1002/ldr.2421

Chapman CA, Chapman LJ (1999) Forest restoration in abandoned agricultural land: a case study from East Africa. Conserv Biol 13:1301-1311. https://doi.org/10.1046/j.1523-1739.1999.98229.x

CIFOR (2013) Hutan dan Mitigasi Perubahan Iklim, Apa yang Perlu Diketahui oleh Para Pembuat Kebijakan. CIFOR Factsheet No 17, Juni 2013. Center for International Forestry Research. Bogor, Indonesia. http://dx.doi.org/10.17528/cifor/004161

Cole RJ, Holl KD, Keene CL, Zahawi RA (2011) Direct seeding of late-successional trees to restore tropical montane forest. For Ecol Manag 261(10):1590-1597. https://doi.org/10.1016/j.foreco.2010.06.038

De Sousa DC, Engel VL (2018) Direct seeding reduces costs, but it is not promising for restoring tropical seasonal forests. Ecol Eng 116:35–44. https://doi.org/10.1016/j.ecoleng.2018.02.019

De Steven D (1991) Experiments on mechanisms of tree establishment in old-field succession: Seedling emergence. Ecology 72(3):1066–1075. https://doi.org/10.2307/1940606

Doust SJ, Erskine PD, Lamb D (2006) Direct seeding to restore rainforest species: microsite effects on the early establishment and growth of rainforest tree seedlings on degraded land in the wet tropics of Australia. For Ecol Manag 234:333–343. https://doi.org/10.1016/j.foreco.2006.07.014

Downer R, Manteuffel-Ross T, Tymon L, Aghai M (2024) Direct seeding for conifer regeneration in the Pacific Northwest: A past, present, and future of operational practices. J For 122(2):171–184. https://doi.org/10.1093/jofore/fvad050

Elliott S, Blakesley D, Hardwick K (2013) Restoring tropical forests: a practical guide. Royal Botanic Gardens, Kew, UK.

Engel VL, Parrotta JA (2001) An evaluation of direct seeding for reforestation of degraded lands in Central Sao Paulo State, Brazil. For Ecol Manag 152:169–181. https://doi.org/10.1016/S0378-1127(00)00600-9

FAO (2005) Forests and floods - Drowning in fiction or thriving on facts? RAP Publication 2005/03 Forest Perspectives 2. Collaboration of Center for International Forestry Research, Bogor and Food and Agriculture Organization of the United Nations, Rome, Italy.

Figueiredo MA, Messias MCTB, Leite MGP, Kozovits AR (2021) Direct seeding in the restoration of post-mined Campo Rupestre: Germination and establishment of 14 native species. Flora 276-277:151772(1–9). https://doi.org/10.1016/j.flora.2021.151772

Frastien D (2017) Perubahan peruntukan kawasan hutan menjadi bukan kawasan hutan untuk menjamin hak masyarakat atas tanah. University of Bengkulu Law Journal 2(2):151-164. https://doi.org/10.33369/ubelaj.2.2.151-164

Fukuoka M (1978) The one-straw revolution: an introduction to natural farming. Rodale Press, Inc., Emmaus, PA, USA.

Gevrek MN, Atasoy GD, Yigit A (2012) Growth and yield response of rice (*Oryza sativa*) to different seed coating agents. Int J Agric Biol 14(5):826–830.

Govinden-Soulange J, Levantard M (2008) Comparative studies of seed priming and pelleting on percentage and meantime to germination of seeds of tomato (*Lycopersicon esculentum* Mill.). Afr J Agric Res 3(10):725-731.

Haase DL, Bouzza K, Emerton L, Friday JB, Lieberg B, Aldrete A, Davis AS (2021) The high cost of the low-cost polybag system: A review of nursery seedling production systems. Land 10:826(1-19). https://doi.org/10.3390/land10080826

Hansen AJ, Neilson RP, Dale VH, Flather CH, Iverson LR, Currie DJ, Shafer S, Cook R, Bartlein PJ (2001) Global change in forests: Responses of species, communities, and biomes: Interactions between climate change and land use are projected to cause large shifts in biodiversity. BioScience 51(9):765–779. https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2

Heiberg SO (1934) Briquette planting. J For 32(3):333-336. https://doi.org/10.1093/jof/32.3.333

Heydecker W, Coolbear P (1977) Seed treatments for improved performance-survey and attempted prognosis. Seed Sci Technol 5:353-425.

Holl KD (1998) Effects of above- and below-ground competition of shrubs and grass on *Calophyllum brasiliense* (Camb.) seedling growth in abandoned tropical pasture. For Ecol Manag 109:187–195. https://doi.org/10.1016/S0378-1127(98)00248-5

Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. Restor Ecol 8(4):339–349. https://doi.org/10.1046/j.1526-100x.2000.80049.x

Hossain F, Elliott S, Chairuangsri S (2014) Effectiveness of direct seeding for forest restoration on severely degraded land in Lampang Province, Thailand. Open J For 4(5):512–519. http://dx.doi.org/10.4236/ojf.2014.45055

Jaiti F, Kassami M, Meddich A, El Hadrami I (2008) Effect of arbuscular mycorrhization on the accumulation of hydroxycinnamic acid derivatives in date palm seedlings challenged with *Fusarium oxysporum* f. sp. albedinis. J Phytopathol 156(11-12):641-646. https://doi.org/10.1111/j.1439-0434.2008.01411.x

Johnson RL (1980) New ideas about regeneration of hardwoods. In: Proceedings of hardwood regeneration symposium, January 29, 1980, Atlanta, GA. Southeastern Lumber Manufacturing Association, Forest Park, GA, USA, pp 17-19.

Juniyanti L, Purnomo H, Kartodihardjo H, Prasetyo LB (2021) Understanding the driving forces and actors of land change due to forestry and agricultural practices in Sumatra and Kalimantan: A systematic review. Land 10(5):463(1-24). https://doi.org/10.3390/land10050463

Jyoti B, Bhandari S (2016) Seed pelleting - A key for enhancing the seed quality. Rashtriya Krishi 11(1): 76-77.

Liptay A, Bolton EF, Dirks VA (1982) A comparison of field seeded and transplanted tomatoes grown on a clay soil. Can J Plant Sci 62(2):483-487. https://doi.org/10.4141/cjps82-068

Louhaichi M, Gamoun M, Ouled Belgacem, A (2021) Direct seeding: a fast and cost-effective method for large-scale restoration of degraded rangelands. R4D Initiatives. Beirut, Lebanon: ICARDA. https://hdl.handle.net/20.500.11766/12231

Maginnis S, Elliott, C (2005) Forests and Natural Disasters. Arborvitae No. 27. The IUCN/WWF Forest Conservation Newsletter. https://iucn.org/sites/default/files/import/downloads/arborvitae27.pdf

Manoharan PT, Shanmugaiah V, Balasubramanian N, Gomathinayagam S, Sharma MP, Muthuchelian K (2010) Influence of AM fungi on the growth and physiological status of *Erythrina variegata* Linn. grown under different water stress conditions. Eur J Soil Biol 46(2):151-156. https://doi.org/10.1016/j.ejsobi.2010.01.001

MoEF (2020a) The state of Indonesia's forests 2020. Ministry of Environment and Forestry, Republic of Indonesia, Jakarta, Indonesia.

MoEF (2020b) Statistik Kehutanan Indonesia Tahun 2020. Kementerian Lingkungan Hidup dan Kehutanan. Ministry of Environment and Forestry, Republic of Indonesia, Jakarta, Indonesia.

MoEF (2021) Updated nationally determined contribution Republic of Indonesia. Ministry of Environment and Forestry Directorate General of Climate Change, Jakarta, Indonesia.

MoEF (2022) Statistik Lingkungan Hidup dan Kehutanan Indonesia Tahun 2022. Kementerian Lingkungan Hidup dan Kehutanan. Ministry of Environment and Forestry, Republic of Indonesia, Jakarta, Indonesia.

MoEF (2024) The state of Indonesia's forests 2024 towards sustainability of forest ecosystems in Indonesia. Ministry of Environment and Forestry, Republic of Indonesia. Jakarta, Indonesia.

Murdiyarso D, Ambo-Rappe R (2022) Rehabilitasi Kawasan Pesisir untuk Mitigasi Perubahan Iklim: Peranan mangrove dan penurunan emisi tingkat sub-nasional, Working Paper 11. Center for International Forestry Research (CIFOR), Bogor, Indonesia.

Nawir AA, Murniati, Rumboko L (Eds) (2007) Forest rehabilitation in Indonesia: where to after three decades? Center for International Forestry Research (CIFOR), Bogor, Indonesia.

Naruangsri K, Pathom-aree W, Elliott S, Tiansawat, P (2024) Selecting suitable tree species for direct seeding to restore forest ecosystems in Northern Thailand. Forests 15(4):674(1-17). https://doi.org/10.3390/f15040674

Neeraj, Singh K (2011) Organic amendments to soil inoculated arbuscular mycorrhizal fungi and *Pseudomonas fluorescens* treatments reduce the development of root-rot disease and enhance the yield of *Phaseolus vulgaris* L. Eur J Soil Biol 47(5):288-295. https://doi.org/10.1016/j.ejsobi.2011.07.002

Nurhasybi, Sudrajat DJ (2018) Seed pellets of *Calophyllum inophylum* and *Enterolobium cyclocarpum* for direct seeding application on degraded lands. In: IUFRO – INAFOR Joint International Conference 2017, "Promoting Sustainable Resources from Plantations for Economic Growth and Community Benefits"– Poster A7, pp 283-288.

Nurhasybi, Sudrajat DJ (2009) Teknik penaburan benih merbau (*Instia bijuga*) secara langsung di hutan penelitian Parungpanjang, Bogor. Jurnal Penelitian Hutan Tanaman 6(4):209-217. https://doi.org/10.20886/jpht.2009.6.4.209-217

Nurhasybi, Sudrajat DJ (2013) Gained experience through direct seeding of several tree species in degraded land in West Java, Indonesia. In: Proceedings of the 2nd INAFOR International Conference of Indonesia Forestry Researchers-August 27-28, 2013. Forest Research and Development Agency, pp 298-308.

Podlaski S, Chrobak Z, Wyszkowska Z (2003) The effect of parsley seed hydration treatment and pelleting on seed vigor. Plant Soil Environ 49(3):114-118. https://doi.org/10.17221/4099-PSE

Priadi D (2010) Aplikasi teknik enkapsulasi pada benih sengon (*Paraserianthes falcataria*). Teknologi Indonesia 33(2):92–99.

Ryu C-M, Kim J, Choi O, Kim SH, Park CS (2006) Improvement of biological control capacity of *Paenibacillus polymaxa* E681 by seed pelleting on sesame. Biol Control 39(3):282-289. https://doi.org/10.1016/j.biocontrol.2006.04.014

Schmaltz EM, Steger S, Glade T (2017) The influence of forest cover on landslide occurrence explored with spatio-temporal information. Geomorphology 290:250–264. https://doi.org/10.1016/j.geomorph.2017.04.024

Stanturf JA, Dumroese RK, Elliott S, Ivetic V, Khokthong W, Kleine M, Lang M, Löf M, Madsen P, Prescott C, Young T (2024) Advances in forest restoration management and technology. In: Katila P, Colfer CJP, de Jong W, Galloway G, Pacheco P, Winkel G (eds), Restoring forests and trees for sustainable development. Oxford University Press, Oxford, UK, pp 297-334. https://doi.org/10.1093/9780197683958.003.0011

Sudrajat DJ, Rustam E, Widyani N, Nurhasybi, Yulianti, Handayani T, Maharani D, Rosdayanti H, Wawangningrum H, Efendi M, Damaiyani J, Suhaendah E, Salim MA, Yuskianti V (2024) Comparison of direct-seeding, bare-root and polybag methods on early growth, root structure and plant establishment cost of mahogany (*Swietenia macrophylla*). Aust For 87(4):151-160. https://doi.org/10.1080/00049158.2024.2411783

Sudrajat DJ, Rustam E, Nurhasybi, Widyani N, Yulianti, Isnaini Y, Aprilianti P, Primananda E, Zanzibar M, Suhartati, Putri KP, Yuniarti N, Surono, Yuskianti V (2023) Improving the success of direct seeding through the application of seed briquettes, aquasorb, and sowing time: case studies on *Ceiba pentandra, Enterolobium cyclocarpum*, and *Calophyllum inophyllum*. For Sci Technol 19(2):130–137. https://doi.org/10.1080/21580103.2023.2198549

Sudrajat DJ, Rustam E (2020) Reforestation by direct seeding of *Gmelina arborea* using seed briquettes: Composition, size and site preparation, and sowing date. IOP Conference Series: Earth and Environ Sci 533:012014. https://doi.org/10.1088/1755-1315/533/1/012014

Sudrajat DJ, Nurhasybi, Suita E, Rustam E, Sawitri R (2019) Teknologi Alternatif untuk Rehabilitasi Lahan dan Hutan: Biopot dan Briket Benih. In: Sawitri R (Ed), Konservasi Kehati Skala Demo-Plot. IPB Press, Bogor, Indonesia, pp 153-184.

Sudrajat DJ, Nurhasybi, Suita E (2018) Comparison of *Nyamplung* plant establishment: direct seeding, bare-root, blocked media, and containerized seedlings. Jurnal Manajemen Hutan Tropika 24(2):51-59. https://doi.org/10.7226/jtfm.24.2.51

Sukra R (2021) Indonesia Siapkan Teknologi Penanaman Mangrove dengan Teknologi Drone. INVESTOR.ID. https://investor.id/business/259773/indonesia-siapkan-teknologi-penanaman-mangrove-dengan-teknologi-drone (last accessed 18 December 2024).

Tamilarasan C, Jerlin R, Raja, K (2021) Seed ball technique for enhancing the establishment of subabul (*Leucaena leucochepala*) under varied habitats. J Trop For Sci 33*(*3):270–276. https://doi.org/10.26525/jtfs2021.33.3.270

Taylor A, Paine D, Suzuki N, Nault B, McFaul A (2002) Coating technologies for seed treatment applications. In: XXVI International Horticultural Congress: issues and advances in transplant production and stand establishment research 631, pp 49-54. https://doi.org/10.17660/ActaHortic.2004.631.5

Tongo A, Mahdavi A, Sayad E (2014) Effect of super absorbent polymer aquasorb on chlorophyll, antioxidant enzymes and some growth characteristics of *Acacia victoriae* seedlings under drought stress. Ecopersia 2(2):571–583. http://ecopersia.modares.ac.ir/article-24-11798-en.html

Tsakaldimi M, Ganatsas P (2016) A synthesis of results on wastes as potting media substitutes for the production of native plant species. Reforesta 1:147–163. https://doi.org/10.21750/REFOR.1.08.8

Wahyunto, Dariah, A (2014) Degradasi lahan di Indonesia: Kondisi existing, karakteristik, dan penyeragaman definisi mendukung gerakan menuju satu peta. Jurnal Sumberdaya Lahan 8(2):81-93.

Wennström U, Bergsten U, Nilsson JE (2007) Seedling establishment and growth after direct seeding with *Pinus sylvestris*: effects of seed type, seed origin, and seeding year. Silva Fennica 41(2):299-314. https://doi.org/10.14214/sf.298

Widyani N, Surono, Sudrajat DJ, Rustam E, Nurhasybi, Putri KP, Yuskianti V (2024) Direct seeding of *Ceiba pentandra* and *Leucaena leucocephala* using seed briquette with AMF and DSE inoculations to support a green economy. IOP Conference Series: Earth Environ Sci 1302:012027. https://doi.org/10.1088/1755-1315/1302/1/012027

Wijaya A, Chrysolite H, Ge M, Wibowo CK, Pradana A, Utami AF, Austin, K (2017) How can Indonesia achieve its climate change mitigation goal? An analysis of potential emissions reductions from energy and land-use policies. Working Paper, World Resources Institute, Jakarta, Indonesia. Available online at www.wri.org/publication/how-can-indonesia-achieve-itsclimate-goal

An overview of seeding methods to restore tropical forests of Brazil

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Abstract

Brazil contains 15–20% of the world's biodiversity, with forests originally covering 88% of its territory, now reduced to about 58%. The country has committed to restoring at least 12 million ha of forests by 2030. Seeding is a cost-effective method for tropical forest restoration, widely used in Brazil, but its effectiveness for species-rich forests is still uncertain due to low establishment rates for many species. Most seeding research has involved relatively few species, and many are short-lived, raising concerns about long-term ecosystem development. Invasive grasses and loss of native species are major barriers to restoration. There is a significant gap between seed demand for restoration and current production capacity. Seed dormancy can be a barrier to rapid establishment; treatments to break dormancy must be tailored to species and site conditions. Large-seeded species and those with certain functional traits (e.g., deep roots, storage cotyledons) perform best. The main sowing methods are broadcast, line, and seeding holes, each suited to different site conditions. *Muvuca* is a notable technique involving a diverse seed mix for large-scale restoration. High sowing rates are often necessary due to low emergence and establishment rates. Fencing and ant control (especially leaf-cutter ants (*Atta* spp. and *Acromyrmex* spp.)) are critical to protect seeds and seedlings from herbivory and physical damage. Ongoing weed control is essential for successful establishment. Seed availability, low establishment rates, and competition with invasive species are the major limiting factors.

Keywords

Atlantic Forest, seed functional traits, ecological restoration, muvuca, seed networks, seed dormancy

Contents

1 Introduction

Brazil, a megadiverse country, hosts an estimated 15–20% of the world's biodiversity. A variety of forests are distributed across six biomes (Figure 1) and originally covered around 88% of its 8.51 million km^2 territory (Oliveira et al. 2022), currently covering about 58% of the total land area (MapBiomas 2023). Most of the present forests are in the Amazon (70%) and the Cerrado (18%) biomes, although all of the terrestrial biomes include some forest areas.

Recognizing the importance of tropical forests to conserve biodiversity and provide ecosystem services, especially carbon sequestration and climate regulation, Brazil has committed to an ambitious target of restoring at least 12 Mha by 2030 (Brasil/MMA 2017). To achieve this, a complex institutional arrangement has been organized involving government, private companies, NGOs, and civil society (Brasil 2012). To comply with the Native Vegetation Protection Law (NVPL), landholders must conserve or restore/rehabilitate up to 20% of the native vegetation in Legal Reserves on their rural property throughout the country, or up to 80% in the Amazon biome. Additionally, Permanent Protection Areas are to be established for stream buffers varying in width from 5 to 100 m depending on watershed characteristics and property size. The total area of native vegetation in these legally protected areas amounts to about 19 to 21 Mha across the country (Soares-Filho et al. 2014; Guidotti et al. 2017). Restoration initiatives have benefited from rapid research advances in the last few decades (Durigan and Engel 2015; Guerra et al. 2020), contributing to ecologically sound approaches and technically effective strategies to restore tropical forests.

Under appropriate conditions, seeding is considered a cost-effective method for tropical forest restoration (Engel and Parrotta 2001; Guerin et al. 2015; Souza and Engel 2023). While this practice is widely applied in Brazil, where it has been extensively studied (Souza 2022), most seeding research, especially early work from the 1980s and 1990s, involved relatively few species (Engel and Parrotta 2001; Guerin et al. 2015), and studies involving a larger number of species have generally reported low establishment rates (Silva et al. 2015; Souza and Engel 2018). Thus, the effectiveness of seeding for restoring species-rich tropical forests is largely unknown, limiting their use on larger scales. Furthermore, as many of the studied species are short-lived, the continued development of forest ecosystems under restoration may be threatened if recruitment of other individuals or species does not occur within the lifespans of the planted species (Bellemo 2017). A larger array of suitable species for various biomes and forest types is necessary for improving the restoration method. This paper is a synthesis of seeding practices for forests in three major biomes of Brazil—the Amazon, Cerrado, and Atlantic Forest, and includes recommendations for practice.

2 The forests

2.1 Physiographic regions

A variety of forest types are distributed across the 6 biomes (Figure 1) that are classified according to climatic zones and local physiographies (IBGE 2012). These include the Amazon (rainforest), Cerrado (tropical savanna), Caatinga (dry forest), Atlantic Forest, Pampa (subtropical grassland), and Pantanal (wetland complex). Of these, we will concentrate on the Amazon, Cerrado, Caatinga, and Atlantic Forest biomes.

The Amazon biome has the largest proportion of forest cover (74%), represented mainly by *Dense Tropical Rainforest* along the Solimões-Amazon River Basin. In this region, the mean annual temperature is approximately 25 °C with low annual thermal amplitude, high precipitation, and typically no dry season. Tree species in the Amazon forest are estimated at 16,000, of which only 1.4% collectively comprise 50% of all individuals (Ter Steege et al. 2013). Although almost 1000 species have timber potential, about 300 have known commercial value and only 20 species (that have been overexploited) comprise more than 50% of the annually extracted timber volume (Andrade et al. 2022). Forests that are flooded seasonally (*Várzea* floodplain forests) or permanently (*Igapó* swamp forests) occur in the lowlands due to the strong influence of river hydrological regimes. Areas not influenced by seasonal flooding support *Terra firme* (upland) forests that are characterized by trees ranging from 30 to 50 m tall, 3 to 4 vegetation layers, high vegetation density and species diversity, and the presence of epiphytes and lianas. The southern and eastern borders of the Amazon Biome (transition zones to the Cerrado and Caatinga Biomes, respectively) are dominated by *Open Tropical Rainforest* which is characterized by a high abundance of palms (Arecaceae), bamboos (Poaceae, subfamily Bambusoideae), and lianas (transition to the Cerrado and Caatinga biomes, respectively).

The Cerrado is the second largest biome in the country, occupying most of the Brazilian central plateaus. It has a mosaic of vegetation types that grade from open grasslands to typical savannas and forested savannas, depending on increasing soil fertility, pH, and organic matter, and decreasing soil acidity, aluminum levels, and fire disturbance (Ribeiro and Walter 2008). Forest cover is around 44% of this biome (Brasil 2019) which holds around 1800 tree species (JBRJ 2024). The typical *Savanna Woodlands (Cerrado strictu sensu)* represents 28% of the area and is characterized by an open, 2-layered canopy up to 5 m tall with a continuous forest floor of shrub, herbaceous vegetation, and grasses. Trees typically have tortuous architecture, thick leaves and bark, and deep roots that often reach the water table. Soils are infertile and acidic, the topography is undulating, and elevation is between 400 to 600 m. Along water courses and streams, riparian and gallery forests occur, forming denser corridors across the landscape. Under more favorable conditions, vegetation encroachment leads to development of 3-storied forests with taller and straighter trees that form a continuous canopy and have no herbaceous/grassy floor (*Forested Savannas* or *Cerradão*), along with semideciduous and deciduous forests (Ribeiro and Walter 2008) These forests correspond to 13% of the total area (MapBiomas 2023).

Northeastern Brazil has a Semi-Arid Tropical climate with high average annual temperatures (23 to 27 °C), low rainfall (<800 mm, some regions with less than 300 mm), a long dry season (6–10 months), and the predominance of shallow, rocky soils (Luvisols, Entisols, and Planosols) that limit plant growth (EMBRAPA 2006). The *Tropical Dry Forest* covers 50% of the Caatinga biome and is characterized by a dense canopy of low stature and highly branched deciduous trees, most of them bearing water-storage structures in stems and roots, and other adapted vegetation such as cacti (Cactaceae) and bromeliads (Bromeliaceae). More than 2000 plant species (including 914 tree species) have been described for this biome (JBRJ 2024), of which 380 are endemic.

The Atlantic Forest biome, which historically covered around 150 Mha, occurs across a wide latitudinal range from 4 to 32 °S (Figure 1) and a broad elevational range from sea level to more than 2700 m (Ribeiro et al. 2009). Considered one of the global biodiversity hotspots (Mittermeier et al. 2011), it hosts more than 20,000 plant species of which almost half are endemic and about 5000 are trees (Lima et al. 2024). Native vegetation currently occupies 26% of the territory, but only 12.6% of the original forest cover remains (MapBiomas 2023; SOS Mata Atlântica/INPE 2023). The Atlantic Forest persists as highly fragmented and degraded remnant stands, of which more than 80% are less than 50 ha (Figure 2) and only 8.5% of the original cover is in forest fragments larger than 100 ha (Ribeiro et al. 2009; SOS Mata Atlântica/INPE 2023).

This biome includes a variety of forest types due to the climatic and topographic variation and continentality. Along a coastal strip varying from 50 to 200 km in width, precipitation is high and well distributed throughout the year due to the maritime influence and orographic effect of the Serra do Mar mountain ranges. This gives rise to *Dense Tropical Rainforest*, in which the canopy reaches 25 to 30 m with some emergent trees, 3 to 4 vegetation layers, and diverse plant life such as epiphytes, palms, and lianas. Composition and structure vary along elevational gradients from Lowland to High-montane Tropical Forests. The *Mixed Dense Rainforest* (Araucaria Forest) covers the meridional plateaus in the subtropical climate zone (warm temperate), with well-distributed rainfall and mild temperatures, as well as disjunct patches occurring at high elevation within the tropical zone and in forest patches in the Pampa biome. Conifers (*Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus lambertii* Klotzsch ex Endl.) dominate the upper and middle canopy, with a high abundance of Lauracea and Myrtaceae species in the subcanopy. *Tropical Seasonal Semideciduous Forests* cover the inland portions of the biome where continentality and topography decrease annual precipitation (1000 to 1500 mm annually) and create a 3- to 4-month dry season. Up to 30–50% of the canopy trees drop their leaves during the dry winter. The *Tropical Seasonal Deciduous Forests* predominate where precipitation is lower and the dry season persists 4 to 6 months within the Atlantic Forest, Cerrado, and Pantanal biomes, or at the border of the Atlantic Forest and Pampa biomes due to cooler winters (Figure 1) (IBGE 2012).

The other two biomes represent a smaller percentage of the territory (Figure 1). The Pantanal wetlands biome occupies a tropical moist seasonal climate, with a dry season of 1 to 3 months. Flooded lowlands surrounded by undulating plateaus are covered with a mosaic of vegetation types including seasonal semi-deciduous and deciduous forests, savannas, and grasslands. In this biome, forests comprise 16% of the area and savanna forms another 16% (MapBiomas 2023). The Pampa biome is mostly open grassland characterized by shallow soils and a warm-temperate climate with mild winters and well distributed rainfall. Forest covers 11% of the biome (MapBiomas 2023): *Araucaria Forests* (Mixed Subtropical Rainforest) occupy scattered patches in deeper soils, and *Subtropical Deciduous Forests* occupy the plateaus between the meridional border of the Atlantic Forest Biome and the grasslands.

2.2 Deforestation and forest degradation

Forest exploitation and deforestation in Brazil have been ongoing since colonial times, starting with export of brazilwood (*Paubrasilia echinata* (Lam.) Gagnon, H.C. Lima & G.P. Lewis) by the Portuguese Crown from Atlantic Coastal rainforests in the 16th century. Several succeeding cycles of natural resource exploitation and deforestation have occurred in the Atlantic Forest Biome for enterprises such as sugarcane (*Saccharum officinarum* L.) and coffee (*Coffea* spp. L.) production, cattle (*Bos taurus*) ranching, and mining of gold and precious gems (Costa 2022). Today, 70% of the Brazilian population lives in this region. Only a small percentage of its original forest remains intact, and deforestation rates in the Atlantic Forest Biome have been declining in recent years (SOS Mata Atlântica/INPE 2023).

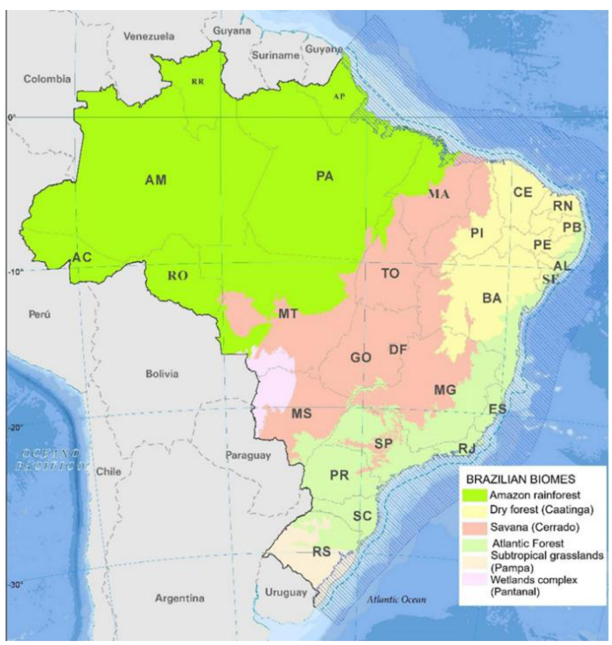

Figure 1. Major Brazilian terrestrial biomes according to IBGE classification. Forests and woodlands are found in all biomes. Two-letter abbreviations denote Brazilian state names. Adapted from IBGE (2024).

Recent deforestation drivers in Brazil include agricultural expansion, infrastructure development, mining, and urbanization. Agricultural expansion, mainly for cattle ranching, is still the main driver of deforestation and the primary source of greenhouse gas emissions in all biomes. Mining has resulted in deforestation over extensive areas, sometimes up to 70 km away from leases (Sonter et al. 2017). Mining activity occupies 150,000 ha in Brazil, 67.6% (101,100 ha) of which are illegal gold mines, mainly in the Amazon region (MapBiomas 2023). Iron and bauxite represent 50% of the total mine lease area; other mined materials include ornamental rocks and limestone (22%); gold (6%), tin and other minerals (nickel, manganese, niobium), together representing around 21.5% of the mined area. Illegal gold mining in the Amazon region has increased sharply in the last few years, and although it represents a small percentage of all deforestation, it is carried out in protected areas and Indigenous lands, causing huge environmental impacts to aquatic ecosystems, including high pollution levels by mercury wastes (Harris 2020).

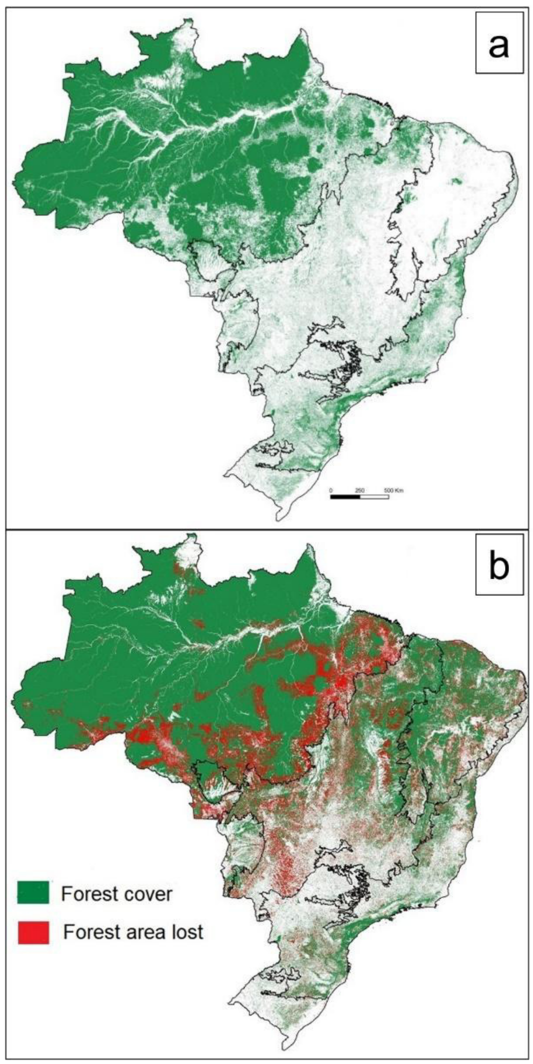

Figure 2. (a) Current forest cover in Brazil (including savanna and dry forest woodlands). (b) Loss of forest cover from 1985 to 2022. Adapted from MapBiomas (2023).

Development of infrastructure such as roads and railroads, waterways, ports, energy plants, and human settlements have resulted in additional forest loss. For example, in the Amazon, almost 95% of all deforestation has taken place within 5 km of roads and waterways (Oliveira et al. 2022). Land grabbing is another deforestation driver, particularly in the Amazon biome, where valuable timber species are illegally harvested from public lands and the residual forest is burned, cleared, and converted to agriculture to claim ownership (Oliveira et al. 2022). This illegal occupation has also increased the frequency and extent of forest fires, as fires used to prepare the felled forest for agriculture or to renew pasture frequently spread into the remaining forest. Climate change is intensifying fire frequency and intensity, creating a loop of degradation particularly in ecosystems not adapted to burning such as Amazonian rainforest and Pantanal wetlands (Pivello et al. 2011; Cardil et al. 2020).

Although deforestation rates have decreased during the last decade, 87.6 Mha of forest have been lost in the last 38 years, 58 Mha of tropical forest and 29 Mha of savanna (Souza et al. 2020; MapBiomas 2023). Recent deforestation due to land use change has been highest in the Cerrado biome (33.8% of the country total and 27% of the biome) and the Amazon (41.8% of the country,13% of the biome), mainly in the regions known as the Arc of Deforestation (Figure 2). During the same period, pastureland expanded by 60%, agriculture by 219%, and forest plantations by 496% (MapBiomas 2023).

To comply with Brazilian legislation, it is estimated that at least 10 Mha of degraded pastureland (1.4 Mha in the Atlantic Forest biome) could be placed under forest restoration without compromising livestock production (Feltran-Barbieri and Féres 2021). Considering that Brazilian pastureland productivity currently functions at one-third of its potential carrying capacity, increasing productivity to 70% of its potential could make an additional 36 Mha available for restoration,18 Mha in the Atlantic Forest Biome (Strassburg et al. 2014).

3 Impacts of deforestation or degradation on restoration sites

3.1 Physical and biotic degradation

The direct impact of deforestation is the immediate loss of plant and animal biodiversity, especially of endemic and rare species. This is particularly important in the Atlantic Forest biome where fragmentation (Ribeiro et al. 2009) and human-induced impacts (Lima et al. 2020) jeopardize plant and animal endemism (40 to 50% of plants and some animal groups in this region are endemic). Atlantic Forest fragments hold up to 31% fewer tree species and 32–42% fewer individuals of late-successional, large-seeded, and endemic tree species relative to low-disturbance forest patches (Lima et al. 2020). Consequently, more than 60% of the 5,000 tree species and 82% of endemic tree species are threatened in this biome (Lima et al. 2024). This high level of habitat fragmentation also threatens biodiversity by hindering gene flow and increasing genetic erosion.

Defaunation due to hunting and habitat fragmentation can have profound effects on the reproductive mechanisms of forest tree species as most tree species depend on biotic agents for pollination or seed dispersal (Howe and Smallwood 1982; Bawa 1990; Jordano et al. 2007). Seed sources are already scarce for many species and propagule dispersal limitations further decrease opportunities for tree colonization in highly deforested/degraded landscapes, especially for late-successional species (Emer et al. 2018; Pires et al. 2023). Dispersal limitations are expected to increase, especially in the Amazon and the Cerrado, and other biomes if current deforestation levels for agricultural expansion continue.

Even where propagule dispersal is not a limiting factor, substrate or microclimate modification in deforested/degraded areas can hinder seed germination and plant establishment. Loss of vegetative cover modifies the microclimate, increasing air and soil temperatures and decreasing relative air and soil humidity, which creates unfavorable conditions for seed germination, especially of late successional species with recalcitrant seed (Souza et al. 2021). Further, loss of vegetative cover increases vulnerability of seedlings in frost-prone areas (Balandier et al. 2009).

Soil erosion and mass transport, e.g., debris flows, can remove or bury seed, create unfavorable substrates for seed germination or root development, remove organic matter and nutrients, and thereby decrease plant growth and productivity. Soil liming followed by heavy fertilization for production of soybean (*Glycine max* (L.) Merr.) and other crops on Cerrado soils can create unfavorable substrates for restoring savanna species but favor biological invasions (Cava et al. 2018). Deforestation followed by soil exposure and poor irrigation practices in dry areas can lead to soil salinization, which arrests recovery of Caatinga vegetation. Burning increases soil organic matter loss, nutrient volatilization, and formation of soil surface crusts that decrease water infiltration, soil water retention capacity, and the soil seed bank.

Invasive non-native grasses are perhaps the most significant barrier to seed germination and seedling establishment at restoration sites. African grasses including several in the genus *Urochloa* spp. P. Beauv., as well as *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs, *Melinis minutiflora* P. Beauv., and elephant grass (*Cenchrus purpureus* (Schumach.) Morrone) are primary invasives on former agricultural and pasture lands throughout the country, but mainly in south, southeastern, and central regions. *Eragrostis plana* Nees, an African grass, is somewhat restricted to the Pampa biome where it outcompetes native species and dominates natural grassland and herbaceous communities. These widespread invasives can modify microclimate, and many ecological processes such as nutrient cycling, and they tolerate fire or even enhance fire probability (D'Antonio and Vitousek 1992; Adelino et al. 2021).

3.2 Seed, seedling, and damaging agents

Seed germination and early establishment in the field are the most vulnerable phases of the tree life cycle (Kitajima and Fenner 2000). Pre- and post-dispersal seed predation, seedling herbivory, and damage by animals and humans are important factors jeopardizing seeding success (Crawley 200). Seed insects, especially beetles and weevils (Order Coleoptera), can damage seed prior to sowing, resulting in decreased germination rates. Insects, birds, and rodents (Order Rodentia) are the main seed consumers, acting in different natural and restored tropical forests. Insects and granivorous birds also predominate in disturbed areas or restored areas (Christianini and Galetti 2007; Villota-Cerón and Engel 2021). Ants (Family Formicidae) of various genera, especially *Atta* spp., are major seed predators, particularly in the Cerrado biome (Vaz Ferreira et al. 2011; Costa el al. 2016). In tropical forests, ants and rodents may actively move or disperse seed and impact plant demography (Christianini and Oliveira 2009, 2010) (Figure 3a) but they can be detrimental at restoration sites. Indeed, we have observed leafcutter ants (*Atta* spp., *Acromyrmex* spp.) actively removing seed from seeded sites, explaining the low recruitment observed for some species that germinate well in nursery tests (Figures 3b, 3c).

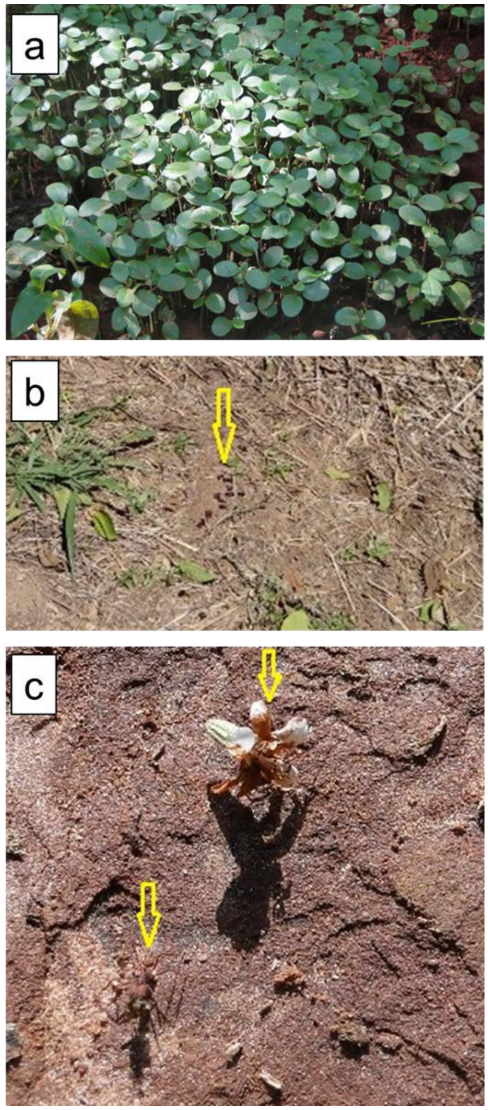

Figure 3. Effects of leaf-cutting ants (*Atta* spp. Fabricius) at restoration sites. (a) Seedlings of *Croton floribundus* Spreng. (Euphorbiaceae*)*, a common species used in restoration plantings in the Atlantic Forest, which have germinated over an ant nest. (b) Seeds of *Anadenanthera colubrina* var*. cebil* (Griseb.) Altschul (Fabaceae), and (c) *Cordia trichotoma* (Vell.) Arráb. ex Steud. (Cordiaceae) being removed by ants from restoration sites. (Photo credits: V.L. Engel).

Leaf-cutter ants are also more damaging to seedlings in open areas than in mature forests due to the abundance of food resources and the lack of natural enemies and competitors. They prefer tender leaves of young seedlings, particularly leaves high in nitrogen and low in secondary compounds such as saponins or the essential oils of *Myrtaceae and Verbenaceae* (Ferreira et al. 2013; Garcia et al. 2020; Villota-Cerón 2020). Leaf-cutter ants also prefer species in particular families such as *Euphorbiaceae, Rubiaceae, and Lecythidaceae* (Garcia et al. 2003).

Grazing domestic animals, mainly cattle and horses (*Equus ferus caballus*), and invasive exotic herbivores, can also cause extensive damage to restoration sites through trampling and grazing. Feral pigs and boars (*Sus* spp.) and European hares (*Lepus europaeus*) are the most harmful exotic species for seeded restoration sites in Brazil. Boar trample over sown sites, uproot seedlings and saplings, and feed on green manure plants and seed (Adelino et al. 2021).

Some of the main abiotic factors affecting seed germination and early seedling establishment include excessive rainfall in areas of wet or monsoon climates (Amazon, Atlantic Forest, and Pantanal biomes) resulting in seeds being carried away in surface water or being buried in sediments. In lowlands with hydromorphic soils and shallow water tables or impermeable clay layers, seed and seedlings can suffer flooding (Pampa biome and other susceptible regions). Although seeding in all regions is usually conducted during the rainy season, in some years the rainy season can be short, or periods of rain can be interspersed with dry and hot periods that jeopardize seed germination. At the southern border of the Atlantic Forest and in the Pampa biome, restoration sites can be exposed to frost during winter months.

4 Mitigating impacts for seeding

4.1 Site preparation

Most seeding areas in Brazil are lightly to moderately degraded former pastures, agricultural lands, or forests plantations being restored for watershed protection or compliance with environmental legislation. In these areas, mechanical site preparation predominates and is preferable, where feasible, because it improves physical conditions for germination and seedling establishment and can better control invasive grasses. In steep terrain, where rock outcrops impede mechanization, or in cases of low-income landowners, site preparation must be done manually, i.e., creating seed beds with hoes, mattocks, or soil augers.

Although seedlings are generally considered to be a more effective strategy for more highly degraded areas such as former mining sites, seeding has shown good results on bauxite mined sites in the Amazon region, given adequate site preparation (Parrotta and Knowles 1999, 2001). This would include machine leveling of the clay overburden, application of about 15 cm of stockpiled topsoil and woody debris, deep (90 cm) ripping of sowing lines (1 m between lines), then sowing on alternate rip lines at a 2 x 2 m spacing.

Mechanical site preparation can be approached in different ways, depending on the levels of soil compaction and grass infestation (Figure 4). On recently cultivated agricultural lands, a single light harrowing will sometimes be sufficient. On former pastureland with high soil compaction and grass infestation, adequate site preparation involves conventional plowing and harrowing the total area, sometimes followed by ripping. Guerin et al. (2015) recommended harrowing three times, every 30 to 40 days to reduce grass germinating from seed in the seed bank. If a very tall grass cover exists, e.g., elephant grass can grow to more than 2 m tall, one or two knife-roller operations may be necessary before plowing or harrowing (Figures 4a, 4b).

Disadvantages of preparing the entire site (Figure 4g) are associated with exposing soil, leading to losses of soil moisture, organic matter, and native herbs and forbs from the soil seed bank. To reduce these losses, minimal tillage practices have been used successfully (Engel and Parrotta 2001; Engel et al. 2002). These involve broadcast spraying of post-emergent herbicides over the area (Figures 4d, 4e and 4f) about 20 days before site preparation to control weeds and form a straw layer on the soil, after which the site can be ripped to break soil compaction and establish seeding rows (Figure 4h). After ripping, it is important to delay sowing until the site receives sufficient rain to transport loose soil into the ripped rows, thereby preventing the sown seed from being subsequently buried. Alternatively, a moldboard plow (Figure 4i), which turns soil over better than a disc plow, can be used instead of ripping to break compacted soil and produce seeding rows.

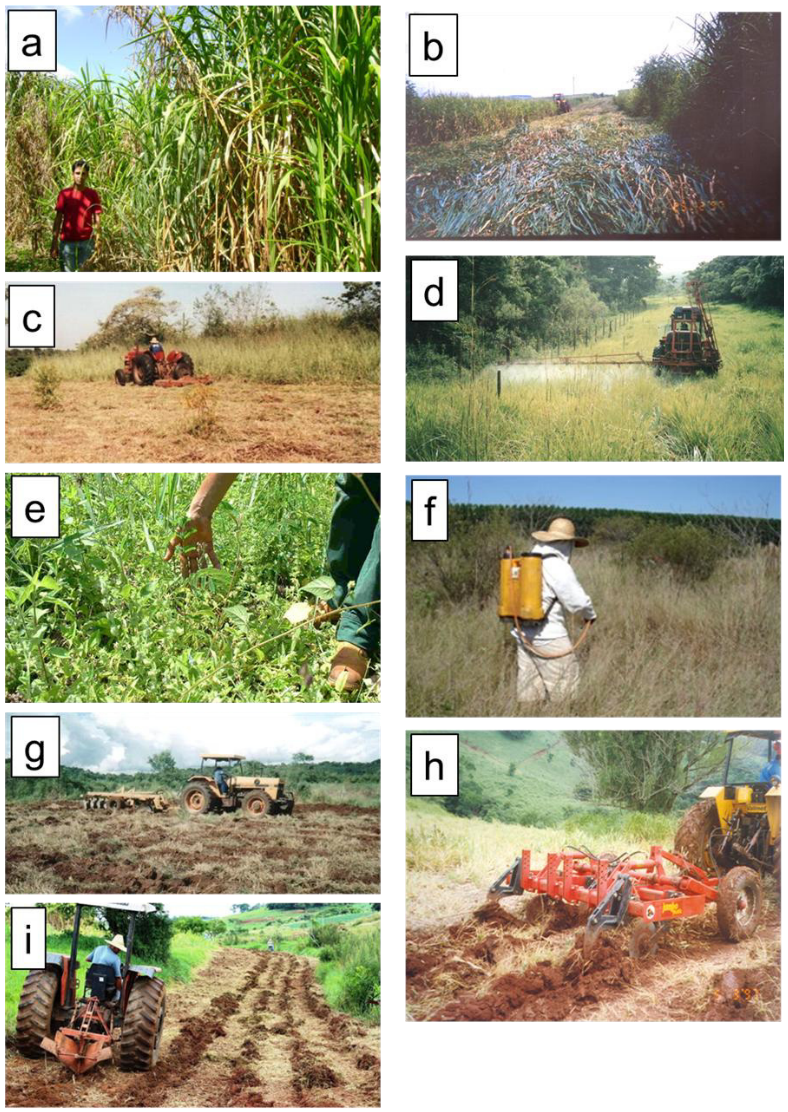

Figure 4. Site conditions and site preparation practices. (a) Elephant-grass (*Cenchrus purpureus* (Schumach.) Morrone), used as forage, can invade fertile soils forming a dense and tall mass that precludes natural regeneration. (b) Elephant-grass control with a knife-roller. (c) Mechanical mowing of *Urochloa decumbens* (Stapf) R. Webster. (d) Mechanical broadcast spraying an entire site with post-emergent herbicide. (e) High richness of herbs and forbs after herbicide application to remove invasive grasses. (f) Backpack spraying. (g) Mechanical plowing an entire area for site preparation. (h) Mechanical ripping a site post-treatment with herbicides. (i) Furrowing with a moldboard plow. (Photo credits: (a–h) V.L. Engel, (i) R.B.G. da Silva).

To reduce post-sowing competition with aggressive grasses, which tends to affect seedling growth more than seedling survival (Passaretti et al. 2020), green manures and cover crops have been widely used in Atlantic Forest and Cerrado restoration, although their effectiveness may be limited if weed infestation is very high (Engel et al. 2002; Guerin et al. 2015; Sampaio et al. 2015; Silva et al. 2015; Rocha et al. 2020a, 2020b). By creating a favorable microclimate, cover crops like the shrubby pigeon pea (*Cajanus cajan* (L.) Huth) can favor seedling height growth while helping to suppress weeds (Silva et al. 2015; Souza et al. 2021). Green manure can also function as bait for leafcutter ants, decreasing damage on the sown trees because they receive higher rates of herbivory than the native plants (Reis et al. 2019).

Herbicides are very effective for controlling invasive grasses, especially when seeding former pasturelands or sites adjacent to pastures. Glyphosate application over the entire restoration site before seeding is a common practice (Figure 4d), with an application rate of 4.5 to 5 L ha^{-1}; mixing urea in the solution can increase foliar absorption. On steep terrain, spraying is conducted manually using backpack sprayers (Figure 4f). Sites with high grass cover (*Urochloa* spp., *Megathyrsus* spp., *Mellinis* spp., and others) should be mowed first then a post-emergent herbicide applied after the grass resprouts (Figure 4c).

Although post-emergent herbicides could have detrimental effects on soil microbiota and potentially affect native plants due to their wide-spectrum activity, the release from grass competition will allow other herbs and forbs already present in the seed bank to become established, increasing soil coverage and increasing plant and insect biodiversity (Figure 4e). The straw layer helps to maintain soil coverage, retaining soil humidity and suppressing the germination of weeds from soil seed banks (Silva and Vieira 2017). To restore open habitats of Cerrado vegetation, a combination of prescribed burning, hoeing, and selective post-emergent herbicide treatment for grasses, e.g., Haloxyfop-R methyl ester, has been the most cost-effective option to control *Urochloa decumbens* (Stapf) R. Webster (Assis et al. 2021).

Pre-emergence herbicides have shown to be very effective in controlling grasses, especially for restoration plantings, but they are not recommended for seeding sites as they have the potential to prevent seed germination of many native species as well (Souza and Engel 2017). More extensive testing of Indaziflam®, which has demonstrated a lower inhibition of native seed germination, has been recommended (Dutra et al. 2023).

Aside from mulching with grass straw (Sampaio et al. 2015; Silva and Vieira 2017), other soil amendment practices are used in Brazilian seeding operations. While liming and chemical fertilization have been traditionally used for restoration plantings, there is little evidence of beneficial effects on seeded sites. However, an evaluation of several seeded sites up to 10 years old indicated that soil with relatively high phosphorus content and base saturation accumulated above ground biomass at twice the rate of lower fertility soils (Freitas et al. 2019). One limitation to more widespread use of soil amendments might be the lack of knowledge of nutritional needs for most tree species used in seeding operations, especially during seedling establishment. Operational issues such as the need to incorporate lime into the soil in advance of seeding can pose additional constraints. There is also evidence that weeds may benefit from fertilization more than desired seedlings because of their higher competitive ability (Silva et al. 2015). Nevertheless, a few experiments that have evaluated slow-release fertilizers, e.g., Osmocote®, show promising results, especially when used with hydrogels (Silva Neto et al. 2020).

4.2 Damage prevention

Seeded restoration sites must be fenced from livestock and other herbivores to prevent physical damage to seed and seedlings and grazing of seedlings, especially on sites adjacent to pastureland or in landscapes susceptible to wildlife damage. While seed and seedling protection against herbivory, soil erosion, or mechanical damage could be accomplished by installing individual transparent plastic shelters just after seedling emergence, this practice has yielded inconclusive experimental results (Ferreira et al. 2007; Malavasi et al. 2010) and the high labor involved in making and installing shelters does not justify broad-scale use. Further, shelters do not seem to offer effective protection against the most important damaging agents in all biomes, i.e., leaf-cutter ants of the genera *Atta* and *Acromyrmex.*

The most common ant control in forestry has been the use of granulated formicide baits (sulfluramide or fipronil), or formicide (liquid, powder or mist nebulization) application directly into ant nests. Bait is preferred because control can be systematic and continuous. Granulated formicide baits should be applied just after site preparation and some weeks prior to sowing, and as often as possible every 1–2 months up to three years.

Bait plants have also been used to reduce seedling predation pressure. For example, sowing tamarind seed (*Tamarindus indica* L.), an exotic fruit tree which suffers high predation by ants, in mixture with native trees reduces predation on the latter (Leão et al. 2022). Sesame (*Sesamum indicum* L.) and castor bean (*Ricinus communis* L.) produce essential oils that affect fungal colonies reared in leaf-cutter ant nests, acting as natural bait (Pereira 2021). These plants can also be sown in mixture or in alternating rows with desirable tree seed where their seedlings function as natural baits.

Post-sowing weed control of seeded areas is generally necessary until the stand develops a closed canopy and light-demanding weeds are no longer competitive. This is usually accomplished with herbicide applications, but this poses risks to desired tree seedlings and other plants even when spray nozzles for precise application (conic spray nozzles or foam nozzles) are used. Additional measures to protect seedlings during herbicide application are often necessary, such as temporary shelters made of bamboo sections or polyethylene nursery containers (Figure 3g).

5 Seed procurement and preparation

5.1 Seed demands and preparation

Considering the very extensive forest area to be restored across all Brazilian biomes, procurement of seed of adequate quality in sufficient quantity is a significant bottleneck. To achieve 12 Mha of restored area by 2030, as pledged by Brazil under the Paris Agreement (Brasil/MMA 2017), the demand for seed of native species over a 10-year period is estimated at 360 to 1,560 Mg yr^{-1} depending on the ratio of active versus passive restoration. Of this seed volume, 2,700 to 14,000 Mg would be required for restoration accomplished through seeding (Urzedo et al. 2020).

The demand for seed cannot be supplied by current production potential. Between 2007 and 2018, six major seed networks in Brazil, encompassing the Atlantic

Forest, Amazon, and Cerrado biomes, produced 416.7 Mg of seeds (34.7 Mg per year) (Urzedo et al. 2019). Other estimates indicate a total production of 180 Mg of native seeds in a 4-year period, from 997 seed collectors belonging to the nine major community-based seed networks, in the same biomes (Padovezi et al. 2024). The development of seed networks in recent years has increased the production capacity and numbers of species being offered. Initiatives started in the Amazon and Cerrado biomes (Schmidt et al. 2019) have expanded to include the Atlantic Forest, Caatinga, and other biomes/regions, resulting in the creation of the Caminhos da Semente (Seed Paths) and Redário Initiative (https://redario.org.br), a market chain hub of all community-based seed networks. The Initiative is a partnership between seed collection groups, through associations and cooperatives of traditional populations (Indigenous and Quilombola communities) and small farmers, currently comprising 27 networks. Around 1200 collectors are expected to procure over 46 Mg of seeds from 176 species yearly, with collection and trading depending on the expected demand. In most situations, pre-ordering well in advance (prior to the main harvesting season of desired species) will be necessary to guarantee adequate supply in quantity and quality.

To meet demands for native seed, expansion and improvement of seed networks are necessary. Although operating throughout the country, not all regions and biomes are adequately represented at present by the seed networks from Redário, notably the Pampa, Pantanal, and Caatinga biomes, as well as the Tropical Seasonal Semi-deciduous and Mixed Subtropical (Araucaria Forest) forests within the Atlantic Forest domain.

Moreover, to meet potential demand, reliance on seed networks alone may be insufficient. Public and private investment in training and capacity building for seed producers can help to ensure high physiological and genetic seed quality. Greater availability of information on provenances and population sizes for each seed lot can improve tracking within seed networks, allowing for adequate matching of genetic sources with restoration areas. Modification of current seed-related policies and regulations is also considered vitally important, including, for example, simplified rules for small producers (<500 kg yr^{-1}) and for seed certification (Redário/CTSF 2023; Schmidt et al. 2019; Urzedo et al. 2019), as well as creation of fiscal and taxation incentives along the seed production chain (Redário 2024).

5.2 Phenology, demography, and genetic considerations in seed production

Timing of seed collection depends on the phenological state of the desired species. Tracking phenology is challenging due to several factors, including the fact that flowering, fruiting patterns, and seed production of many tropical forest species are highly variable between years. These phenological traits also vary between and within biomes (Engel and Martins 2005; Ferragutti 2021).

Most trees in tropical regions are either fleshy fruited species dispersed by animals predominantly during the rainy season, or wind or self-dispersed species that bear dry fruit with seed dispersed during the dry season or during the transition to the rainy season (Knowles and Parrotta 1997; Howe and Smallwood 1982). However, in Cerrado ecosystems where rainfall is strongly seasonal, seed dispersal and dormancy are timed such that germination is optimized, i.e., with the onset of the rains. Species lacking seed dormancy disperse seed at the end of the dry season, while those exhibiting some level of seed dormancy can disperse in other periods of the year, as the seed is able to maintain viability during the less favorable period (Oliveira 2008; Salazar et al. 2011; Escobar et al. 2018). Wind-dispersed, non-dormant seeds are dispersed and germinate only during the rainy season, while animal-dispersed seeds are dispersed throughout the year, depending on the dormancy level (Escobar et al. 2018). Nevertheless, species showing rainy season seed dispersal tend to have recalcitrant seed that are difficult to store—this may explain why seed inventories in markets and seed sown in restoration projects are biased towards species with orthodox seed that disperse during the dry season (Pellizzaro et al. 2017).

Further, fruit should be collected upon ripening, or as close to maturity as possible in the case of dehiscent fruits or others that cannot be collected after they fully ripen. Thus, collectors need to be familiar with the fruiting process and phenology of the species they wish to collect to avoid losing seed that was collected prematurely or seed that dispersed before they could be collected. Such variability in fruiting and seed dispersal patterns as well as dormancy characteristics pose significant challenges for planning, seed collection, and maintaining seed stock inventories.

The inclusion of an adequate number of species and genetic diversity within species in seed collection programs is also a challenge, particularly in tropical forests where most tree species are naturally rare, and many have restricted ranges or aggregated population distributions. For example, in the Amazon forest, less than 300 of the estimated 16,000 tree species are hyper-dominant; all others are considered very rare (Ter Steege et al. 2013). Moreover, irregular fruiting or low fruit loads, multilayered canopies, and tall trees make seed collection very difficult within mature dense forests. As a result, seed collection tends to be restricted to more open habitats, forest edges, forest fragments, or isolated trees, which can compromise seed quality because of the higher self-fertilization risks and lower genetic variability as compared to in forest interiors (Aleixo et al. 2021). In contrast, in Cerrado and Caatinga biomes where more open savannas predominate, seed collections tend to be easier because trees are shorter, exhibit high fruiting seasonality (Escobar et al. 2018; Oliveira 2008), and higher tree fecundity and seed loads than in closed forests.

Long-term sustainability of plant populations and communities resulting from restoration projects depends not only on species diversity being reached over time, but also on the genetic diversity of the propagules. Nevertheless, establishing tree populations that are genetically diverse and appropriate to the restoration site has rarely been considered due to several constraints (Jalonen et al. 2018; Thomas et al. 2014).

To guarantee adequate genetic diversity, seed sourcing is critical. Firstly, larger patches of habitat are preferred for seed collection because they hold larger populations of most tree species. However, in the Atlantic Forest biome, with its long history of settlement and high fragmentation, large forest patches hosting large tree populations are mostly confined to protected areas, where seed collection has just recently been regulated (Souza et al. 2024). Forest patches available for seed harvesting are mostly located on private properties, are typically less than 50 ha in size (Vancine et al. 2024), and are usually degraded due to exploitive logging of the most valuable timber species, fire, and/or defaunation from hunting. Consequently, these accessible tree populations could be genetically poor and more vulnerable to the negative effects of seed harvesting on native population dynamics, including decreased plant recruitment (Thomas et al. 2014). Thus, given the growing demand to support large scale restoration, overexploitation of seed in Atlantic Forest fragments may contribute to the long-term decline in the genetic diversity of those populations.

To protect wild populations from such decline, it is recommended that annual seed harvests be limited to 20% of the seed produced in each season (Pedrini et al. 2020) and that *ex-situ* seed production areas or orchards be established for species with the most degraded natural populations (Masuthi et al. 2023; Pedrini et al. 2020). Nevertheless, the large-scale use of the same provenances or provenance mixes, for instance, from seed orchards can also lead to reduced genetic variability and selection of particular genotypes (Thomas et al. 2014).

One key aspect to inform seed source selection is the genetic structure of the candidate tree population. Previous research indicates that most genetic variability occurs between populations at a small-scale (or populations from different forest fragments), and not within populations (Hamrick and Loveless 1986; Mijnsbrugge et al. 2010). To ensure adequate genetic diversity within the species used for restoration purposes, seed collection needs to be meticulously planned to ensure high genetic variability for many species, preservation of genetic structure for a species, and minimal risks to natural populations. Also, guidelines for the operation of seed networks should reinforce traceability and prescribe careful labeling of seed batches, including the specification of seed provenance, a record of genetic sampling of wild collections, as well as rules for subsequent processing of the seed (Mijnsbrugge et al. 2010; Pedrini and Dixon 2020).

Literature from Brazil recommends that collections are made in 10 to 30 matrices per species with at least 100 m between individuals or sub-populations (Brancalion et al. 2015; Aleixo et al. 2021; NEMA/UNIVASF 2022). This is not adequate for some species. For example, *Myracrodruon urundeuva* Allemão (Anacardiaceae) is widely distributed in the Atlantic Forest, Cerrado, and Caatinga biomes, but with very low population densities that have been overexploited. For genetic conservation and restoration programs involving this species, a minimum of 50 mother trees spaced at least 5.2 km apart would be considered necessary (Moraes et al. 2005). For adequate genetic conservation and at larger restoration scales, a collection of 45–60 individuals is typically necessary for avoiding genetic bottlenecks and assuring conservation of rare genes (Vencovsky 1987; Freire et al. 2007; Piña-Rodrigues et al. 2007). It is obviously difficult to ensure proper sampling for all species in large-scale seed collection programs, but these considerations serve to inform improvement of existing collection schemes.

To help reconcile different seed-provenance principles of reproducing natural gene flow and genetic diversity along with predicting future climatic adaptation, the Climate-Oriented Seed-Sourcing Tool (COSST) has been proposed (Silva et al. 2025). This tool allows identification of optimal areas for collecting seed and estimates the proportion of seeds to be sourced from various suppliers, using species occurrence and climatic data. It supports seed-sourcing decisions made by practitioners and identifies seed collection priority areas for seed suppliers.

5.3 Seed collecting, handling and storing

Once matrices are marked and the proper collection period is established, appropriate collection techniques will be determined by fruit or seed characteristics, the matrices, and the ecosystem to be sampled. For species with dry indehiscent fruit, collection can be done directly on the ground just after dispersal. For species with dehiscent fruit, collection must be done directly from the tree before the fruit splits open. This is accomplished with pruning poles, by climbing, or in the case of large trees, segmented ladders or tree climbing equipment.

Several guides can be referenced for best handling and storage techniques for various tropical tree species (Schmidt 2000; Vozzo 2002; Piña-Rodrigues and Balistiero 2015; Souza Jr. and Brancalion 2016; Ferraz et al. 2019; Albuquerque et al. 2022). According to those guides, seed processing should be based on species-specific requirements for ensuring germination, reducing barriers to germination in the field, or preparing them for storage. Processing will vary for each species according to the morphological, physiological, and ecological characteristics of the seed. Seed processing is normally carried out manually because of the difficulty in mechanizing different approaches for the diversity of seed that are highly variable in shape, size, structure, and collection system.

Procedures depend on seed traits (Piña-Rodrigues and Balistiero 2015). For seed borne in dehiscent dry fruits, it is first necessary to open the fruit to expose the seed for extraction. This can typically be done by placing the fruit in the sun or in greenhouses with forced circulation. For indehiscent dry fruits with winged seeds, processing could be unnecessary if the seed can be sown directly into the soil. Indehiscent dry fruits that need to be opened to extract seed from pulp can be processed similarly to dehiscent fruits. Seeds can be extracted from fleshy fruits by using sieves and running water, while seeds with a hard endocarp, such as palms, are processed using cutting or cracking tools. While these are general procedures for seed processing, there are many species with seeds that necessitate unique and specific processing methods. Also, seed of some species do not require processing and can be sown in the same condition as collected.

Proper storage is essential for maintaining seed viability and vigor. Although it may be ideal to sow seed immediately after it is collected, this is not always possible because seed maturation and optimal sowing times rarely match (Albuquerque and Moraes 2022). For example, seed dispersed at the end of the rainy season usually have to be stored until the following summer. Also, much of the seed collected in Brazil must be stored because it is moved through seed networks.

Suitable storage conditions are highly variable, but storage protocols generally focus on species tolerance to desiccation, that is, whether seed is orthodox or recalcitrant (Vozzo 2002; Piña-Rodrigues and Balistiero 2015). Orthodox seed have low moisture content when collected and can be stored for a relatively long time because they tolerate drying if kept under low temperature and humidity. Recalcitrant seed has a high moisture content when collected and does not tolerate drying or exposure to low temperature. It typically needs to be sown soon after collection to avoid loss of vigor but does remain viable if temporarily stored in polyethylene bags inside a cold chamber or domestic refrigerator. Thus, the use of recalcitrant seeds in seeding projects is challenging unless their dispersal time coincides with sowing or they exhibit dormancy. Nevertheless, many tropical and subtropical tree species (about 10–15% of them) can be classified as intermediate, tolerating storage at around 10% humidity at 15°C (Pieruzzi 2022).

Maximum length of storage is highly variable depending on the physiological condition of the seed and storage conditions. Recalcitrant seed remains viable for only a few weeks to a few months after harvest, while orthodox seed can remain viable for years if stored under adequate conditions. For example, in the Atlantic Rainforest, species have been classified into 7 storage classes, varying from those that can be stored for more than 2 years, those that can be stored for months or weeks, and ephemeral species that cannot be stored at all (Albuquerque and Moraes 2022). For the seasonal deciduous forest of central Brazil, several tree species keep viability after being stored in natural conditions for up to 15 months, which benefits planning for seeding (Lima et al. 2008).

5.4 Seed dormancy

Seed dormancy is an important mechanism that enables dispersed seeds to remain viable for long periods of time under natural conditions (Alves et al. 2022) and matching dispersal time with the most favorable season for germination (Escobar et al. 2018). However, it can be an obstacle for seeding, as seeds sown on restoration sites are expected to germinate quickly and uniformly to facilitate site management in the first years after sowing. Treatments are typically needed to break seed dormancy for some species, and techniques that are used will depend on the type of dormancy (Piña-Rodrigues and Balistiero 2015).

Physical dormancy, typical of seed with a hard coat that prevents air and water from moving into the seed for initiation of the germination process, can be broken through mechanical or chemical scarification methods, i.e., physical abrasion, immersion in hot water, or chemical corrosion of the seed coat to facilitate water absorption and gas exchange. Physiological dormancy, which involves prevention of germination by physiological factors and/or germination inhibition compounds, can be broken by soaking seed in a hormone solution, e.g., gibberellic acid, or leaching of germination inhibitors by soaking the seed in water.

Pereira et al. (2013), who evaluated six native tree species, identified treatments to decrease time to emergence and increase emergence rate of most tested species. For some Cerrado palms such as macaúba (*Acrocomia aculeta* (Jacq.) Sweet), seed can take years to germinate without treatment to break dormancy (Oliveira et al. 2013). Nevertheless, in many cases decreasing germination or emergence time will be advantageous only if the environmental conditions during sowing are very favorable. For example, in the case of a dry spell occurring just after the sowing, most seeds that had started the germination process will not thrive.

Recent studies have demonstrated that treating seeds to break dormancy is not always beneficial for many species. Germination was not hastened for most of the 10 forest and savanna tree species tested by Correia et al. (2021), and they observed high mortality for some species which they attributed to compromised protection from environmental factors that resulted from the breakdown of fruit structures or seed coats.

6 Establishment

6.1 Species selection

The careful selection of species to be seeded in restoration projects is crucial to successful and cost-effective stand development. Tree species richness is very high across Brazil: up to 16,000 species in the Amazon (Ter Steege et al. 2013), almost 5,000 in the Atlantic Forest (Lima et al. 2024), around 1,800 in the Cerrado, over 900 in the

Caatinga, and over 200 in both the Pantanal and Pampa (JBRJ 2024). However, only 254 species from 48 families have been evaluated in seeding projects (Souza 2023). Among these, 70% were tested in one or two studies, while 30% (76 species) were tested in three or more studies. More than half (57%, 43 species) showed establishment rates (defined as the percentage of established seedlings in the field in relation to the number of seeds sowed) below 10%, and only 16 species (21%) showed establishment rates above 20% (Appendix 1).

The continued use of many species that have demonstrated poor field performance may reflect a bias towards species with copious fruiting, higher seed loads, easier harvesting, or good nursery performance rather than field seeding performance. Some species have been recommended in seed mixes traded by seed networks for "muvuca" plantations (see seeding methods below) but without verification of expected results. For example, a comprehensive species list prepared by restoration practitioners (available at: https://www.caminhosdasemente.org.br/especies) included 783 tree and palm species from all biomes. Of the 783 species, only two had not been tested in a nursery setting, two had low or very low emergence (<10%), six had regular emergence (10 to 49%), and all others showed emergence over 50% in nurseries. The same list, however, indicates that 70% of the species (552) have not been assessed under field conditions and of those that had been tested, 143 species showed < 10% emergence in the field, 43 species showed between 10 and 19% emergence, 38 species showed between 20 and 39% and only 7 species showed 40 to 60% emergence.

Some seed and seedling functional traits have proven to be important for selecting potential species for seeding. Seed size and seed mass are among the most important traits that contribute to high germination and survival in the field (Knowles and Parrotta 1995; Camargo et al. 2002; Silva and Vieira 2017; Passaretti et al. 2020; Souza and Engel 2018, 2024; Laumann et al. 2023). Large seeds have high nutrient reserves that can be utilized in early growth, to develop deep roots that grow below roots of weeds, and to better tolerate periods of drought or other stress (Passaretti et al. 2020). Large seeds also have a lower probability of being buried, or carried off by water, wind, or ants. They also take longer for imbibition, protecting them from losing viability due to dry spells during the rainy season (Laumman et al. 2023). Seed shape also affects emergence, with round seeds having better performance than flat ones (Silva and Vieira 2017; Laumann et al. 2023). Another trait considered important for species selection is cotyledon function. Cotyledons play a critical role in seedling establishment and species with storage cotyledons have an advantage over species with photosynthetic cotyledons that rely on external resources for energy (Souza and Engel 2024). For Cerrado restoration, species with seedlings that produce long roots have a greater chance of surviving the dry season and compete stronger with invasive grasses, so they show relatively high establishment when seeded (Passaretti et al. 2020).

In summarizing studies on tropical forest species used to restore forest cover on land mined for bauxite, Knowles and Parrotta (1995) reported that about 21% of the 160 taxa studied could be successfully established with seeding. Those that could be most efficiently established by seeding were restricted to a subset of taxa with relatively large seed (>2 cm long and broad). Three categories of species considered highly suitable for seeding include: (a) full-sun tolerant species that could be established immediately after site preparation, such as *Spondias lutea* L., *Caryocar villosum* (Aubl.) Pers., *Hevea brasiliensis* (Willd. ex A.Juss.) Müll. Arg., *Hevea guianensis* (Aubl.), *Joannesia heveoides* Ducke, *Dypteryx magnifica* (Ducke) Ducke, *Dipteryx odorata* (Aubl.)

Forsyth f., *Hymenaea courbaril* L., *Hymenaea intermedia* Ducke, *Schizolobium parahyba (*Vell.) S.F. Blake, *Enterolobium maximum* Ducke, and *Parkia gigantocarpa* Ducke; (b) species that survive open conditions but prefer shaded conditions when young, such as *Caryocar glabrum* (Aubl.) Pers., *Acioa longipendula* (Pilg.) Sothers & Prance, *Bertholletia excelsa* Bonpl., and *Carapa guianensis* Aubl.; and (c) shade tolerant species suitable for seeding in established restoration forests to increase tree diversity, including *Licania micrantha* Miq., *Endopleura uchi* (Huber) Cuatrec., *Vantanea guianensis* Aubl., *Vantanea paraensis* Ducke, *Lecythis corrugata* subsp. c*orrugata* Poit., *Lecythis pisonis* Cambess., *Swartzia polyphylla* DC., *Vouacapoua americana* Aubl., and *Brosimum potabile* Ducke.

6.2 Plantation design and sowing techniques

Design of stands in seeding projects has included three main approaches: (1) broadcast sowing, (2) sowing in lines (rows), and (3) sowing in seeding holes (Guerin et al. 2015; Sampaio et al. 2015; Amaral et al. 2018; Rocha et al. 2020b; Vieira et al. 2020). This is usually determined by the type of forest to be restored, site degradation level, site characteristics (soil erodibility, topography), landscape structure (size, number, and connectivity of habitat patches), and land use.

Broadcast sowing has been most recommended for use on plains or smoothly undulating terrain, usually associated with more open habitats such as Savanna and Caatinga Dry Forests. Advantages of broadcast sowing are found in time efficiency, a relatively low cost, and the resulting high stand densities (Amaral et al. 2018; Freitas et al. 2019). It is also considered suitable for sites previously used for agriculture, where the occurrence of invasive grasses is low, given the difficulty of post-sowing weed control with herbicides where trees are not in rows. Disadvantages of broadcast sowing include a lower establishment rate relative to sowing density and poor control over spatial distribution of species and individuals.

Site preparation is usually mechanized (disc plowing/harrowing) over the entire restoration area, and sowing can be manual or, more often, mechanized (Figure 5). Light harrowing is recommended after sowing to incorporate seed into the soil. Broadcast sowing can include from one to several dozen species. Mechanized broadcast sowing techniques have been increasingly used for Cerrado restoration. One such technique called “muvuca,” originally developed by Instituto Socio Ambiental (ISA), has been used to restore forests in the Xingu River Headwaters (Campos-Filho et al. 2013; Guerin et al. 2015). The name muvuca indicates a species-rich mix that includes seeds of native trees and perennial/sub-perennial green manure species that are delivered in an inert material such as sand, saw dust, or mineral soil with a lime or grass seed spreader (Figures 6a, 6b). More recently, several adaptations of this technique have been used across other regions and biomes. Broadcast sowing, usually in association with nucleation plantations (islets consisted of dense plantings established with seedlings, *sensu* Holl et al. 2020), has been used for Caatinga dry forest restoration with seed mixes of at least 3 well-adapted tree and shrubby species in either low density (36 seed m^{-2}) or high density (65 seed m^{-2}) (NEMA/UNIVASF 2023).

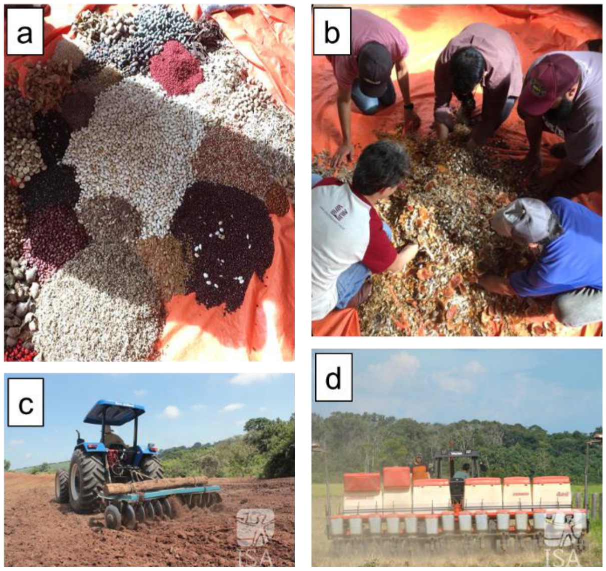

Figure 5. (a) and (b) Preparation of "muvuca" seed mixes for sowing. (c) Harrowing to incorporate sown seed into soil after broadcast sowing. (d) Mechanized broadcast "muvuca" seeding with a soybean (*Glycine max* (L.) Merr.) planter. (Photo credits: (a, b) R.B.G. da Silva; (c, d) by ISA, https://acervo.socioambiental.org/).

Figure 6. (a) Mechanical line sowing using minimum cultivation and a 3-line crop planter. (b) Seed mix using graphite as an inert anti-clogging material. (c) Seed sown on a soil furrow. (d) Manually sowing seed by hand in a furrow. (e) Manual sowing with a hand tool. (Photo credits: (a–c, e) V.L. Engel; (d) R.B.G da Silva).

Line sowing is appropriate for various types of forests and steep terrain because it promotes water infiltration and minimal surface erosion. Other advantages of this method include greater control of spacing and plant composition and application of more flexible planting designs, e.g., different species groups can be assigned to different lines and distance between lines can be adjusted to obtain different plant densities. Also, weed control may be easier because machinery can operate between sowing rows.

Site preparation on relatively flat terrain can be across the entire area using conventional plowing and/or harrowing, or minimal tillage with mechanical ripping or furrowing (with a moldboard plow) can be used on steeper sites. Sowing can be manual or mechanized in either case. Where the entire area is site prepared, mechanized seeding can be conducted with end-wheel grain drills. Sowing lines are generally separated by about 50 cm and the seed mix (muvuca) or monospecific sets being placed inside the hoppers relative to seed size (Figure 6). Another option is mechanical liming machines that are adapted by removing the spreader. This tool will release seed directly from the hopper in a single line (Sampaio et al. 2015). An advantage is that these machines allow the use of seed up to 15 cm wide, while grain drills only accept seeds 1 to 2 cm wide (Campos-Filho et al. 2013). In either case, seeded lines can be on a wide spacing to allow mechanical mowing between rows.

For sites that have received minimal tillage, sowing can be done with minimal cultivation disc planters (Figure 6a). These machines have flexible widths, with 3 to 6 sowing lines and distance between lines of 0.45 to 1 m. Ripping tines can be modified in a way that shallow ripping is conducted simultaneously to cutting the dry straw with the coulter. Seed or seed mixes are placed inside the hoppers and the hopper aperture and operating speed are calibrated for the desired seed density (Engel et al. 2002). Seed can be mixed with powder graphite to avoid clogging (Figure 8b), or with inert material such as sand to improve sowing uniformity (2 parts seed to 1 part fill material) (Engel et al. 2002; Cava et al. 2016). Rows can alternate between tree seed mixes and green manure species (Figure 6a) (Engel et al. 2002).

Adapting machinery for mechanical sowing to accommodate heterogeneous mixes of tree seed can be challenging. Many tree seeds are either too large or too small for conventional apertures on planting machines designed for agricultural crops, resulting in variable release of seed. A solution for this is to use fertilizer hoppers (with large holes) for large seed or complementing mechanical sowing with manual sowing of large, flat, or thin seeds (Engel et al. 2002; Campos-Filho et al. 2013).

Manual seeding can be the best approach for very steep sites or as a complementary method to mechanical seeding for large seeds. Ripping or furrowing the site prior to sowing is not necessary because soil can be broken manually with hoes. Sowing can be conducted by hand or with manual planters depending on seed size (Figures 6c, 8d). Manual seeding has been the preferred technique for areas of water table recharge in the Alto Rio Pardo region, in Northern Minas Gerais state, a transition area between the Cerrado and the Caatinga. In this region, furrows are opened manually with hoes every 3 to 12 m, native grasses are sown between rows, and 18 to 27 native species are sown in the rows (Rocha et al. 2020a).

Seeding hole sowing is practiced on steep sites where mechanized operations cannot be performed, or on very erodible soils where soil disturbance must be minimized. Due to the required labor, this approach is applicable to small areas, such as for enrichment sowing used in combination with other methods, or in cases where additional sowing is needed, such as to stock areas of poor germination or high seedling mortality.

Seeding holes can be opened with motorized augers or manual diggers combined with hoeing around the holes. During digging, it is important that a high volume of soil be pulled out of the hole, which can be mixed with organic matter or fertilizers to increase porosity and form a good seed bed. Vieira et al. (2020) recommend hoeing rows between 90 cm to 1.5 m wide to facilitate digging, turning over soil to 20 to 50 cm deep, and retaining soil inside the holes. Seed beds must be lower than the soil surface to promote water infiltration. Spacing among seeding holes will depend on site characteristics such as degradation level, potential for natural regeneration, and the type of maintenance desired. For example, mechanical mowing requires at least 3 m between holes. Seeding within seeding holes can be accomplished by hand or with manual seeders. Chemical weeding with post-emergent herbicides immediately before or soon after sowing will help control invasive grass competition and will promote better seedling establishment.

6.3 Species numbers

Stands established through seeding have historically used few species. Souza and Engel (2023) noted that more than 90% of the plantations on experimental restoration sites in Brazil were comprised of fewer than 20 tree species. For many of these studies, most species did not emerge or survive to the seedling stage, resulting in species richness levels lower than planned (Engel and Parrotta 2001; Araki 2005; Martins 2009; Meli et al. 2018; Souza and Engel 2018). In the Amazon forest region, only 33 of 160 tested taxa were successfully established by seeding on reclaimed bauxite mines (Knowles and Parrotta 1995). In Caatinga Dry Forests, these numbers are even lower, around three to five species (NEMA 2023).

Low numbers of suitable species and low field establishment seems to be the current rule for seeding on restoration sites in Brazil (Engel et al. 2002; Cava et al. 2016). This is due to the low potential of many species to establish when sown under field conditions, including species that perform well in nurseries (Souza and Engel 2018). For example, Sampaio et al. (2007), Guarino and Scariot (2014), Aguirre et al. (2015), and Meli et al. (2018) seeded 4, 12, 8, and 16 species, respectively, but only 2, 4, 2, and 4 species, respectively, showed establishment rates above 10%. For this reason, it has been proposed that seeding is best utilized on areas in the landscape that would allow for additional subsequent colonization of the site through natural regeneration (Engel and Parrotta 2001; Rodrigues et al. 2019).

More recently the number of species used in field studies has increased, due to growing interest in seeding for large-scale restoration, the development of seed networks, and the enhancement of field research with many species (Pellizzaro et al. 2017; Oliveira et al. 2019; Silva et al. 2019; Liaffa 2020; Vieira et al. 2020). For instance, an average of 70 species, including 15 to 20 pioneer species plus 30 to 60 late successional species, have been used in muvuca plantings at Xingu River Basin (Campos-Filho et al. 2013; Freitas et al. 2019). But failure to establish seedlings is common in these more recent studies and fewer than 30% of the species have survived after 6 years (Guerin et al. 2015). Nevertheless, early development of a dense canopy cover can provide favorable conditions for colonization through natural regeneration, which can comprise as much as 60 to 72% of the species found on mechanically seeded sites (Campos-Filho et al. 2013; Cava et al. 2016; Rodrigues et al. 2019).

6.4 Cover crops, green manure, and hydrogels

Cover crops and plants established for green manure (Figure 8) have been extensively used in seeding projects across biomes to promote early soil cover and to function as nurse plants for regeneration established through sowing (Figure 7). This temporary cover can reduce negative impacts of weed competition and adverse soil or microclimate conditions that hinder emergence and initial development of native plants (Souza et al. 2021), and act as bait for leafcutter ants (Reis et al. 2019). Interplanting native trees with annual cover crops such as corn (*Zea mays* L.) can provide up to 60% ground cover during initial phases of establishment and can provide additional income to farmers (Silva et al. 2015).

Frequently used green manure plants are nitrogen-fixing herbs or shrubs from the Fabaceae; for example, pigeon pea, jack-bean (*Canavalia ensiformis* (L.) DC.), *Crotalaria juncea* L., *Mucuna deeringiana* (Bort) Merr., *Dolichos lablab* L., and others. These can be included as part of a seed mix for broadcast or line sowing or sown in alternate lines with trees. At Xingu River Basin, 6 *Crotalaria juncea* seed, 1 pigeon pea seed, and 3 jack-bean seeds were sown per square meter (100,000 seeds ha^{-1}) (Campos-Filho et al. 2013; Guerin et al. 2015). Engel et al. (2002) sowed about 6.3 jack-bean and 29 pigeon pea seeds per linear meter (21,000 and 19,100 seeds ha^{-1}, respectively) while mechanically line sowing with minimum cultivation.

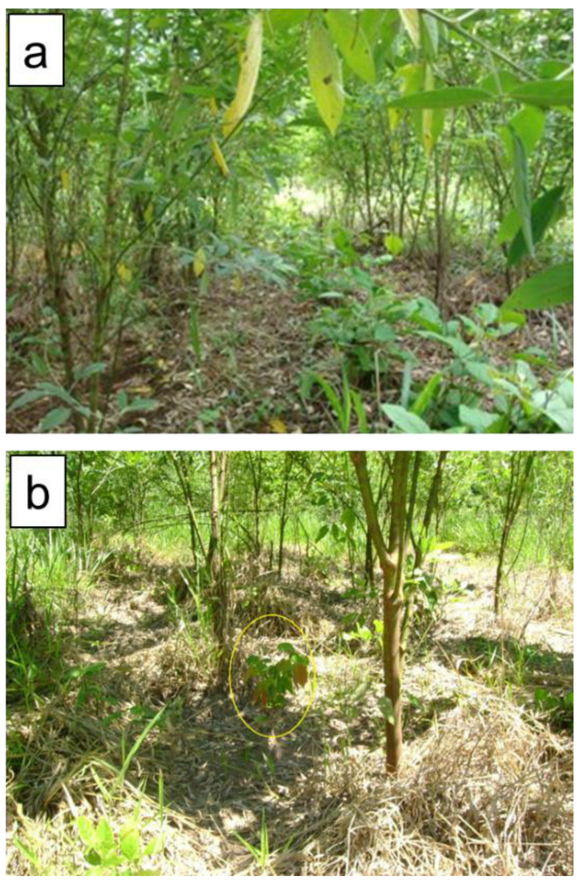

Figure 7. Beneficial effect of green manure plants established with seeded tree species. (a) The quick-forming canopy of pigeon pea (*Cajanus cajan* (L.) Huth) that was sown in alternating lines with tree species. (b) A seedling of a climax species, *Hymenaea courbaril* L. (Fabaceae), under the shade of pigeon pea plants. (Photo credits: V.L. Engel).

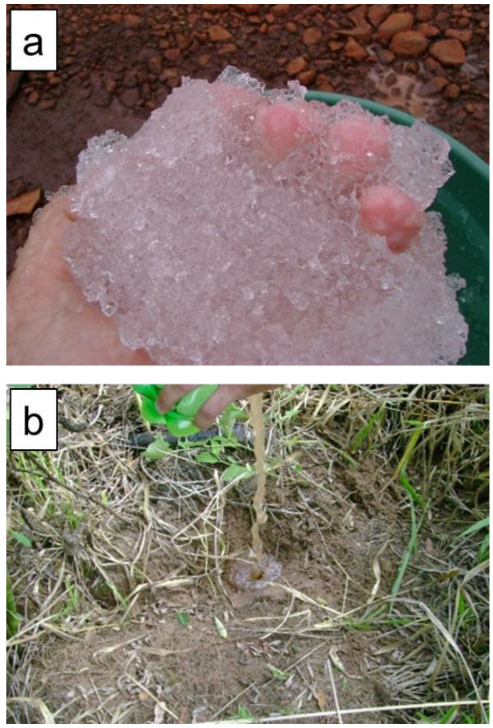

Figure 8. Hydrogel amendment during sowing. (a) Hydrogel solution prepared for application; (b) hydrogel application into the seeding hole. (Photo credits: D.C. de Souza).

To restore forest and meet an objective of 100% soil coverage in five years, Vieira et al. (2020) recommend sowing rates of as much as 415,000 seed ha^{-1} for mechanical broadcast seeding of 13 perennial and semi-perennial species (including green manure and other native bushy species and lianas), 344,000 seed ha^{-1} for line seeding, and 203,850 seed ha^{-1} for cover planting.

Studies of different combinations of cover crop species have shown variable results regarding effects on the development of seeded species. Neutral (Bellemo 2017; Souza et al. 2021), positive (Bourlegat 2020), and negative (Campos-Filho et al. 2013) effects on seedling establishment and/or growth have been reported. Although green manure plants have positive effects on weed control and can provide up to 80% soil cover during the first 6 months, a high density of these plants may increase competition for water and nutrients with negative effects on seedling growth or germination of pioneer and early successional species (Engel et al. 2003; Campos-Filho et al. 2013; Guerin et al. 2015; Souza et al. 2021). Such negative effects might be mitigated by mowing or mulching these plants at a particular stage or when they begin to compete with target species.

Hydrogel (water-absorbing polymers) amendments (Figure 8) can help overcome low water availability and soil humidity problems during the germination phase, given their capacity to hold large volumes of water and water-soluble nutrients that are later released into the rhizosphere. They have been successfully used in forestry and restoration applications with seedlings but remain poorly documented for seeding operations. Results thus far have shown neutral or negative effects (Souza et al. 2021; Silva Neto et al. 2020). It is possible that hydrogels compete with tree seed or seedlings for soil water during dry periods. depending on soil physical properties, soil climate, and hydrogel characteristics.

6.5 Sowing density

Sowing rate can directly impact seeding results. Because most species exhibit very low emergence and establishment rates, high sowing rates are typically necessary to ensure sufficient plant densities for vegetation recovery. More than 50% of the seeding studies conducted in Brazil sowed more than 100,000 seed ha^{-1}, and about 20% sowed more than 500,000 seed ha^{-1} (Souza and Engel 2023). Sowing rates of 145,000 to 1,666,000 seed ha^{-1} were reported for seasonal semi-deciduous forest, but with very low establishment and survival after 3 years (Souza and Engel 2023). At the Xingu River Basin, the 20 to 40 seed m^{-2} muvuca mix corresponded to 200,000 to 400,000 seed ha^{-1}. For the Cerrado-Amazon transition, more than 286,000 seed ha^{-1} are recommended for broadcast or line seeding and 214,000 seed ha^{-1} for seeding of seeding holes (Vieira et al. 2020). For Caatinga Dry Forests, sowing rate can surpass 1,000,000 seed ha^{-1} when mechanical broadcast seeding (360,000 seed ha^{-1} of the cover species *Senna uniflora* (Mill.) H.S. Irwin & Barneby combined with 650,000 seed ha^{-1} of other species) (NEMA 2023).

Sowing rate for a given species will depend on the level of soil coverage or plant density desired and the germination potential of seed. Because rates are typically weight-based, it is important to know the number of seeds per unit weight. Number of seed kg^{-1} for a species is usually provided by seed vendors (as is germination potential) or it can be obtained from the literature. Nevertheless, germination and establishment under field conditions are extremely variable, and some species have been reported to have 0% establishment, despite good germination in nurseries (Appendix 1).

6.6 Sowing depth

Sowing depth can directly affect seedling emergence of species seeded in restoration projects. Seeds deposited on the soil surface or sown at shallow depths have less contact with soil and are subject to adverse weather conditions such as rain, wind, and sudden changes in temperature and humidity (Minami 2010), but can be favored by mulching (Ferreira and Vieira 2024). Seeds sown at depth are under more favorable environmental conditions but need sufficient reserves for the seedling to emerge above the soil surface (Villalobos et al. 2009; Ferreira and Vieira 2024). While seeds of photoblastic species, such as *Croton* spp. L., *Cecropia* spp. Loefl. and *Trema* spp. Lour., require exposure to sunlight to break dormancy, recalcitrant species lose germinative capacity when exposed to the dry conditions of the soil surface (Pieruzzi 2022; Alves et al. 2022). For these reasons, the use of a uniform sowing depth (particularly in mechanized operations) is problematic for species with different requirements. Although more laborious, manual seeding can allow for better control of sowing depth. Typically, large and round seeds should be buried, medium-sized orthodox seeds can be incorporated into the soil, and flat or small seeds should be sown on the soil surface (Silva and Vieira 2017).

The need to incorporate seed into soil with light harrowing is variable and depends on seed traits of the different species being sown (Guarino and Scariot 2014). Soil incorporation may not affect the emergence of round seeded species but negatively affects flat seeded species and those with phanerocotylar epigeal photosynthetic cotyledons (seeds that emerge from soil during germination and expose cotyledons that are foliaceous, capable of photosynthesizing) (Silva and Vieira 2017). Therefore, it is important to consider functional traits of the species to be sown when determining appropriate sowing depth.

6.7 Sowing season

The rainy season in Brazil, a country of continental dimensions, varies substantially by geographical region. Some biomes have a relatively long rainy season, such as the Amazon, while others have a relatively long dry season, such as the Caatinga. With a tropical climate prevailing over most of the country, rains are concentrated in mid-spring to late summer (October to March). However, rainfall is evenly distributed throughout the year in the southern region where a subtropical climate prevails.

Because seeding success is highly dependent on water availability for seed germination and initial seedling survival, seeding typically follows rainy periods. Most Brazilian seeding studies (63%) were installed at the beginning and during the rainy season (Cabin et al. 2002; Souza 2023). The few cases of seeding that were conducted during the dry season required irrigation to ensure success, and this increased implementation and maintenance costs, which decreased operational feasibility (Santos 2010; Santos Jr et al. 2010; Oliveira 2013).

There is a research gap regarding the effect of different sowing periods on emergence, establishment, survival, and growth of sown tree species. On the one hand, seedlings from seeds sown at the onset of the rains will have a relatively long period of adequate water availability, but also high weed competition. On the other hand, seedlings from seeds sown in the middle or at the end of the rainy season will experience less weed competition, but a shorter period of water availability. Souza and Engel (2018), who studied sowing in January and November, found the average establishment of seeds sown in January was higher than those sown in November. This was attributed to a lower level of competition with invasive grasses during seed germination. Future studies with the same species being sown in different sowing seasons (beginning, middle, and end of the rainy season) are needed to evaluate these effects more fully.

7 Establishment

Maintenance of seeded sites, especially those that are broadcast seeded, can be more difficult than stands established with seedlings because of the small size of recent germinants. As discussed earlier, the greatest risks associated with seeded sites are ant herbivory, grazing by livestock, invasive weeds, and fire. Control of leaf-cutting ants with granulated baits must be systematic during the first three years of the restoration project. Fencing should be inspected frequently and repaired when necessary. Maintenance of firebreaks around the site is critical.

Competition from exotic weeds should be controlled by maintenance operations carried out as often as needed. This will typically be every month for the first 3 months, followed by once every 3 to 4 months. Manual hoeing can be done around seeding spots where mechanical or semi-mechanical (using brush or weed trimmers) mowing is used between sowing lines. Grass straw should be mulched around seedling root collars to reduce moisture loss and weed germination. Chemical weeding broad-spectrum post-emergent herbicides, e.g., glyphosate, can be made using backpack sprayers. For these applications, seedlings can be protected using polyethylene containers or bamboo covers (Figure 9). Pre-emergent herbicides that are effective in controlling grasses, such as isoxaflutole, oxyfluorfen, diuron, and atrazine, are not recommended because they can also affect germination of native tree species (Souza and Engel 2017). Additionally, other native herbs and forbs do not seem to harm the newly established seedlings, and should not be removed, as they help to promote soil cover, microclimate, and herbivory protection (Engel et al. 2002; Engel 2011) (Figure 4e).

In geographical regions prone to low night-time temperatures, seedlings can be subjected to frost injury. Late-successional forest tree species have a higher risk of frost injury than species from more open habitats (savannas and grasslands) and from the *Araucaria Subtropical Forest* (Atlantic Forest domain), which tend to have higher frost resistance due to their relatively large root reserves, ability to resprout, and/or other physiological mechanisms. In areas where the risk of low temperatures exists, it is very important to promote quick establishment of vegetative cover, either using cover crops/green manure or less aggressive grasses, like *Megathyrsus* spp. The lack of vegetative cover will increase the chances of frost injury to seedlings, or of high insolation during the day in tropical regions. In some instances where a protective cover has not formed before the winter, it is better to delay weeding because the grass cover can help protect seedlings.

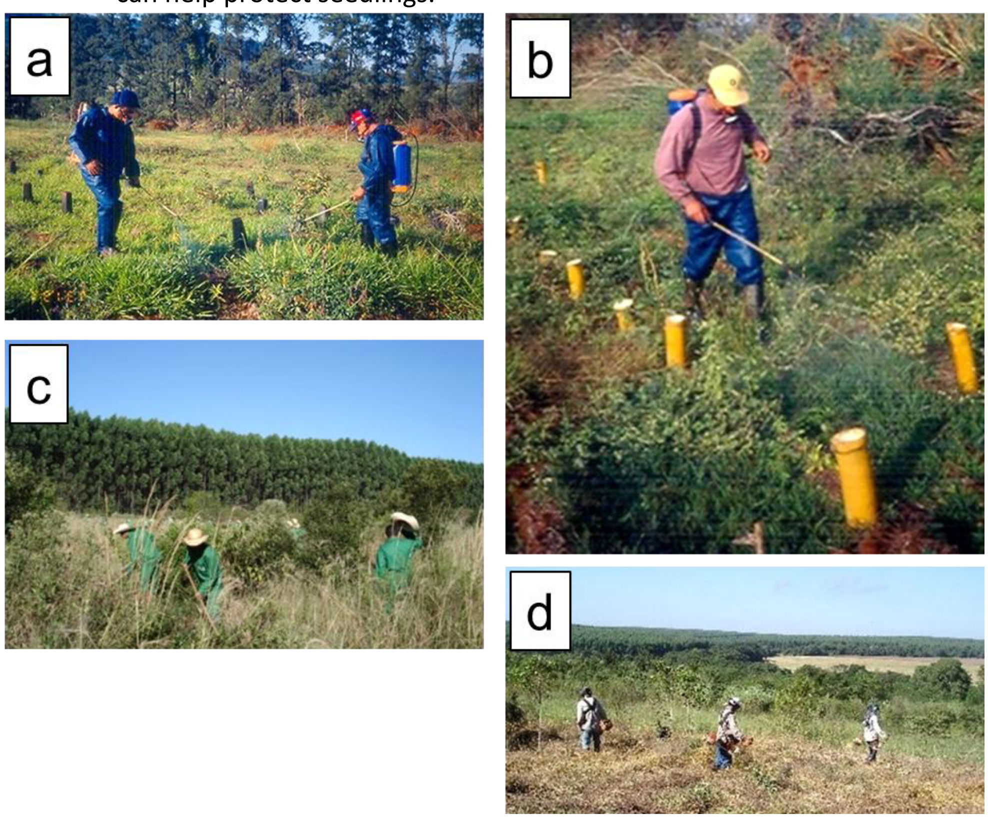

Figure 9. Post-sowing maintenance on seeded restoration sites. (a) and (b) illustrate post-emergent herbicide applications in which seedlings are protected with temporary shelters. (c) Manual hoeing around seedlings. (d) Semi-mechanized mowing with brush and weed trimmers. (Photo credits: V.L. Engel).

8 Successful seeding

8.1 Success criteria and indicators

In any restoration project, success criteria will depend on clearly defined restoration goals. Among proposed monitoring protocols, some people focus on indicators of ecosystem attributes while others include a series of ecological, socioeconomic, and management criteria, indicators, and metrics for different restoration phases (Ruiz-Jaen and Aide 2005; Viani et al. 2018; Oliveira et al. 2021). For any of these approaches, plant survival and growth, canopy cover, coverage and density of invasive grasses, and presence of native species have been prioritized for initial and short-term phases; establishment and maintenance costs are also factors (Oliveira et al. 2019). The lower cost of seeding methods relative to planting seedlings is considered to be one of the greatest motivations for adoption of seeding by landholders (Engel and Parrotta 2001; Campos-Filho et al. 2013; Souza and Engel 2018; Raupp et al. 2020).

For seeding, some specific short-term success indicators should apply at the species level, such as the emergence (proportion of seedlings emerged per number of seed sown 3 months after seeding); establishment rates (percentage of surviving seedlings, usually at 12 months, relative to the number of seed sown); survival rate (percentage of surviving seedlings after 12 months relative to number of emerged seedlings 3 months after seeding or at the first monitoring period); and height growth (Souza and Engel 2023). An index that weighs ecological success by financial costs is useful for decision making between different methods The Species Ecological–Economic Performance Index is one example that can be obtained by dividing the Species Performance Index (SPI) by the total cost per plant spot (or seeding hole) (Ferreira et al. 2023).The SPI corresponds to the product of emergence, survival, and height increment at a certain age. When the emergence rate is not available, the index can be adapted by using the product of survival (%) and height mean increment (m) (Ferreira et al. 2023). In addition to monitoring the restoration site, assessing these indicators helps to improve species selection, sowing methods, and efficiency of seeding in future restoration projects. Additionally, survival and stocking of the regenerating forest are important for predicting the future trajectory of stand structure.

For monitoring a site, species composition and number of sown seed per species are necessary information for evaluating emergence and establishment rates, and for assessing sowing rates for each species needed to produce the desired stand density and species diversity. Also, intermediate and long-term monitoring is important for assessing successional trajectories of seeding methods relative to other methods. This should also include some additional indicators such as native species richness and diversity, native species density and cover, and status of invasive grass cover (Chaves et al. 2015). To achieve the desired species richness typical of tropical forest ecosystems, forest stands created through restoration practices can optimally catalyze regeneration of other native species by facilitating arrival and establishment of natural propagules from trees and forests elsewhere in the landscape and reducing or eliminating biotic or abiotic stressors that hinder or prevent natural regeneration in degraded ecosystems (Parrotta et al. 1997; Engel and Parrotta 2001; Durigan et al. 2010; Rodrigues et al. 2019). For this approach, establishment of a small number of well-adapted tree species might be sufficient to reduce barriers impeding natural succession. So, long-term monitoring of the metrics for natural regeneration in addition to those of sown species will benefit assessment of this objective.

Some protocols for rapid ecological assessment of restored sites have been proposed. The Caminhos da Semente (Seed Paths) Initiative proposes a qualitative and quantitative assessment that includes floristic surveys of the total area plus plot surveys (in five transects of 1 x 20 m per site) of cover crops and woody species seedling density (Ferreira et al. 2020). Soil cover and seedling/sapling height are monitored by the point interception method in 21 points established systematically over the 20-m lines. In the case of mandatory or legal compliance initiatives, a simplified monitoring protocol has been proposed, regardless of the restoration method. The approach involves defining adequacy levels for monitoring periods from 3 through 20 years for the following indices: (a) ground cover of native vegetation (percentage); (b) density of native plants spontaneously regenerating (number of individuals ha^{-1} with height (H) >50cm and circumference at breast height (CBH) <15 cm); and (3) number of spontaneously regenerating native plant species (number of species with H>50cm and CBH<15 cm) (Chave et al. 2015).

Emergence and establishment rates for seeded species are highly variable and difficult to assess, particularly because the exact number of seed sown is rarely known (Doust et al. 2008; Tunjai and Elliott 2012; Campos-Filho et al. 2013b; Meli et al. 2018; Souza and Engel 2018; Freitas et al. 2019). This emphasizes the need for longer monitoring periods, especially when seeding relatively few species. While relatively long monitoring periods are common in forests restored through other methods, most seeding projects in Brazil have included monitoring only in the first 3 to 5 years of establishment (Miranda Neto et al. 2012; Suganuma and Durigan 2015; Garcia et al. 2016; Cava et al. 2018; Souza and Engel 2023). Because of the young age of most plantations, few intermediate and long-term studies have been conducted in tropical forests restored through seeding (Souza 2022). Some studies reporting results through year 10 have shown variable results, especially for sites over 6-years-old, because sowing rate varied up to 200% between sites and initial emergence rates were not reported (Campo-Filho et al. 2013; Freitas et al. 2019).

8.2 Limiting factors and risks

Despite the advancement of native seed collection and production initiatives over the last two decades, seed availability remains a primary limitation to reaching forest restoration goals through seeding methods (Schmidt et al. 2019; Urzedo et al. 2020). The lack of seed or high market costs of available seed have limited the number of species used and the upscaling of restoration projects (Silva 2019; Urzedo et al. 2020), especially in the Atlantic Forest biome. There are many barriers that restrict seed availability and increase collection cost in natural ecosystems, including a limited number of individuals and populations, short periods of viable seed availability, easily dispersed seeds, seeds with maturity at different times, populations located in difficult-to-access locations, and high interannual variability in seed production (Broadhurst et al. 2016), as discussed earlier (Phenology, demography, and genetic considerations in seed production). Therefore, seed collection is a challenging process, and the collected seed must be used carefully to avoid wasting time, money, and genetic material.

Early establishment is the most critical period for success of seeding projects in Brazilian forests because the low establishment rates common to this method appear primarily as a result of low seedling emergence rates (Meli et al. 2018). Reasons for low emergence rates include inadequate microclimatic and soil conditions, competition with invasive species (mainly grasses), seed desiccation and predation, low soil water availability, poor seed quality (Cabin et al. 2002; Malavasi et al. 2005; Doust et al. 2006, 2008; Balandier et al. 2009; Guarino and Scariot 2014; Giacomini 2016; Magalhães 2017; Souza and Engel 2018), and poor site management (Ferreira and Vieira 2024).

Restoration success depends on rapid growth and rapid coverage of soil by the sown species so that microsite conditions are unfavorable for germination and establishment of invasive grasses (Durigan et al. 2013; Durigan and Engel 2015) and favorable for native species regeneration (Parrotta et al. 1997). Infestation of degraded areas by invasive grasses (*Urochloa decumbens*, *Megathyrsus maximum* Jacq., *Melinis minutiflora* P. Beauv., *Andropogon gayanus* Kunth, *Urochloa humidicola* (Rendle.) Morrone & Zuloago, among others) is a primary obstacle to success of seeding projects (Sampaio et al. 2007; Durigan et al. 2013; Passaretti et al. 2020). Consequently, grass control is the main pre- and post-sowing action required on sites occupied by these invasive species (Silva et al. 2015; Pellizzaro et al. 2017; Silva and Vieira 2017).

Good soil coverage can be obtained from adjusting optimal seeding densities for each planted species, which depend again on seed availability and seed costs, given the low emergence rate of most species (Meli et al. 2018). However, growth rates during the first months after sowing can be lower than those observed for planted seedlings (Aragão 2009; Oliveira 2013; Silva 2019), as seedlings can benefit from being taller and having more roots when outplanted. For example, only 2 of 6 species tested had a higher growth rate and biomass accumulation when seeded, as compared to planted seedlings (Ferreira et al. 2023). Thus, in some instances, the choice for seeding will depend on a cost-effectiveness analysis (Meli et al. 2018) and evaluating an option of planting seedlings along with sowing well adapted species of high establishment rate, for example, large-seeded species can be the choice for obtaining fast coverage of soil and optimal survival.

Experience in Brazil has shown that seeding is a very promising approach that needs improvement to be applicable on larger scales. Seeding can be the most suitable restoration method whenever: (a) seedling production or transportation is difficult or expensive, (b) there is an availability of large amounts of seed produced locally by trustworthy sources and at a low cost, and (c) a minimum soil coverage provided by a set of well-adapted species sown will be enough to catalyze natural regeneration by native species from adjacent natural forests in the landscape. We also suggest that seeding can be used also to complement planting nursery-raised seedlings to enhance stand density and diversity of suitable species. While this method is promising, further research to improve establishment and growth of seeded species and development of initiatives to enhance quantity and quality of seed supplies are needed to further advance seeding for ecological restoration, without negatively impacting conservation of natural forests and tree populations.

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10 References

Adelino JRP, Heringer G, Diagne C, Courchamp F, Faria LDB, Zenni RD (2021) The economic costs of biological invasions in Brazil: a first assessment. NeoBiota 67:349–374. https://doi.org/10.3897/neobiota.67.59185

Aguirre AG, Lima JT, Teixeira J, Gandolfi S (2015) Potencial da semeadura direta na restauração florestal de pastagem abandonada no município de Piracaia, SP, Brasil. Hoehnea 42(4):629–640. https://doi.org/10.1590/2236-8906-04/RAD/2015

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22(6):711–728. https://doi.org/10.1127/0941-2948/2013/0507

Albuquerque NCB, Moraes CE, Souza MR, Barros RLC, Alves KA, Pieruzzi FP (eds) (2022) Sementes florestais da Mata Atlântica: um guia para o manejo de espécies da Hileia Baiana Teixeira de Freitas, BA. Programa Arboretum de Conservação e Restauração da Diversidade Florestal, Teixeira de Freitas, Brazil

Albuquerque NCB, Moraes CE (2022) Chapter II.3 - Classificação de sementes florestais nativas da Mata Atlântica quanto ao potencial de armazenamento para o manejo. In: Albuquerque NCB, Moraes CE, Souza MR, Barros RLC, Alves KA, Pieruzzi FP (eds) Sementes florestais da Mata Atlântica: um guia para o manejo de espécies da Hileia Baiana. Programa Arboretum de Conservação e Restauração da Diversidade Florestal, Teixeira de Freitas, Brazil, pp 104–111.

Amaral WG, Pereira IM, Amaral CS, Araújo FV, Titon M, Machado ELM (2018) Chapter 8 - Semeadura direta na restauração ecológica da Mata Atlântica. In: Pereira IM (ed) Restauração florestal da Mata Atlântica: aspectos ecológicos e silviculturais. UFVJM, Diamantina, Brazil, pp 333–370.

Andrade M, Santos H, Nunes F, Costa JN, Lentini MW (2022) Produção de madeira e diversidade de espécies arbóreas exploradas na Amazônia brasileira: situação atual e recomendações para o setor florestal (8; Timberflow: A Plataforma Da Madeira). https://www.imaflora.org/noticia/estudo-inedito-mostra-que-2-das-especies-disponiveis-compoe-mais-da-metade-da-exploracao-madeireira-na-amazonia-brasileira (last accessed 8 August 2024).

Aragão AG (2009) Estabelecimento de espécies florestais nativas, em área de restauração ciliar no Baixo Rio São Francisco. MSc Dissertation, Universidade Federal de Sergipe, Sergipe, Brazil. 61 pp.

Araki DF (2005) Avaliação da semeadura a lanço de espécies florestais nativas para recuperação de áreas degradadas. MSc Dissertation, Universidade de São Paulo, Piracicaba, Brazil. 150 pp. https://doi.org/10.11606/D.91.2005.tde-15072005-142942

Assis GB, Pilon NAL, Siqueira MF, Durigan G (2021) Effectiveness and costs of invasive species control using different techniques to restore cerrado grasslands. Restor Ecol 29(S1):1–9. https://doi.org/10.1111/rec.13219

Balandier P, Frochot H, Sourisseau A (2009) Improvement of direct tree seeding with cover crops in afforestation: Microclimate and resource availability induced by vegetation composition. For Ecol Manag 257(8):1716–1724. https://doi.org/10.1016/j.foreco.2009.01.032

Bawa KS (1990) Plant-pollinator interactions in tropical rain forests. Annu Rev Ecol Syst 21:399–422.

Bellemo AC (2017) Formação de dossel no curto prazo, como estratégia de restauração florestal. MSc Dissertation, Universidade de São Paulo, Piracicaba, Brazil. 85 pp. https://doi.org/10.11606/D.11.2017.tde-27032017-173551

Bourlegat JMG (2020) Avaliação do efeito de diferentes micro-habitat no processo de restauração ecológica da Floresta Estacional Semidecidual. PhD Dissertation, Universidade de São, Piracicaba, Brazil. 127 pp. https://doi.org/10.11606/T.11.2020.tde-18052020-130202

Brancalion PHS, Gandolfi S, Rodrigues RR (2015) Restauração florestal. Oficina de Textos, São Paulo, Brazil.

Broadhurst LM, Jones TA, Smith FS, North T, Guja L (2016) Maximizing seed resources for restoration in an uncertain future. Bioscience 66(1):73–79. https://doi:10.1093/biosci/biv155

Brasil/MMA (2017) Planaveg: Plano nacional de recuperação da vegetação nativa. Ministério do Meio Ambiente/Ministério da Agricultura, Pecuária e Abastecimento/Ministério da Educação, Brasília, Brazil.

Cabin RJ, Weller SG, Lorence DH, Cordell S, Hadway LJ (2002) Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve. Biol Conserv 104(2):181–190. https://doi.org/10.1016/S0006-3207(01)00163-X

Camargo JLC, Ferraz IDK, Imakawa AM (2002) Rehabilitation of degraded areas of Central Amazonia using direct sowing of forest tree seeds. Restor Ecol 10(4):636–644. https://doi.org/10.1046/J.1526-100X.2002.01044.X

Campos-Filho EM, Costa JNMN, Sousa OL, Junqueira RGP (2013) Mechanized direct-seeding of native forests in Xingu, central Brazil. J Sustain For 32(7):702–727. https://doi.org/10.1080/10549811.2013.817341

Cardil A, Miguel S, Silva CA, Reich PB, Calkin D, Brancalion PH, Vibrans AC, Gamarra JG, Zhou M, Pijanowski BC (2020) Recent deforestation drove the spike in Amazonian fires. Environ Res Lett 15:121003. https://doi.org/10.1088/1748-9326/abcac7

Carvalho PER (2003) Espécies arbóreas brasileiras (Vol. 1). Embrapa Informação Tecnológica, Brasília, Brazil.

Carvalho PER (2006) Espécies arbóreas brasileiras (Vol. 2). Embrapa Informação Tecnológica, Brasília, Brazil.

Carvalho PER (2008) Espécies arbóreas brasileiras (Vol. 3). Embrapa Informação Tecnológica, Brasília, Brazil.

Cava MGB, Pilon NAL, Ribeiro MC, Durigan G (2018) Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas. J Appl Ecol 55(3):1164–1172. https://doi.org/10.1111/1365-2664.13046

Cava MGB, Isernhagen I, Mendonça AH, Durigan G (2016) Comparação de técnicas para restauração da vegetação lenhosa de Cerrado em pastagens abandonadas. Hoehnea 43(2):301–315. https://doi.org/10.1590/2236-8906-18/2016

Chaves RB, Durigan G, Brancalion PHS, Aronson J (2015) On the need of legal frameworks for assessing restoration projects success: new perspectives from São Paulo state (Brazil). Restor Ecol 23(6):754–759. https://doi.org/10.1111/REC.12267

Christianini AV, Galetti M (2007) Spatial variation in post-dispersal seed removal in an Atlantic forest: Effects of habitat, location and guilds of seed predators. Acta Oecol 32(3):328–336. https://doi.org/10.1016/j.actao.2007.06.004

Christianini AV, Oliveira PS (2009) The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna. Oecologia 160(4):735–745. https://doi.org/10.1007/S00442-009-1349-2

Christianini AV, Oliveira PS (2010) Birds and ants provide complementary seed dispersal in a neotropical savanna. J Ecol 98(3):573–582. https://doi.org/10.1111/J.1365-2745.2010.01653.X

Correia MRM, Ferreira MC, Alves M, Consolaro HN, Vieira DLM (2021) Less is more: Little seed processing required for direct seeding in seasonal tropics. New For 53:695–712. https://doi.org/10.1007/s11056-021-09881-y

Costa ZPO (2022) Uma história das florestas brasileiras. Editora Autêntica, Belo Horizonte, Brazil.

Costa AN, Vasconcelos HL, Bruna EM (2016) Biotic drivers of seedling establishment in Neotropical savannas: selective granivory and seedling herbivory by leaf-cutter ants as an ecological filter. J Ecol 105:132–141. https://doi.org/10.1111/1365-2745.12656

Crawley MJ (2000) Chapter 7 - Seed predators and plant population dynamics. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, 2nd ed, CABI Publisher, Wallingford, UK, pp 167–182.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol System 23(1):63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Doust SJ, Erskine PD Lamb D (2006) Direct seeding to restore rainforest species: microsite effects on the early establishment and growth of rainforest tree seedlings on degraded land in the wet tropics of Australia. For Ecol Manag 234(1–2):333–343. https://doi:10.1016/j.foreco.2006.07.014

Doust SJ, Erskine PD, Lamb D (2008) Restoring rainforest species by direct seeding: tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. For Ecol Manag 56(5):1178–1188. https://doi.org/10.1016/j.foreco.2008.06.019

Durigan G, Engel VL, Torezan JM, Melo ACG, Marques MCM, Martins SV, Reis A, Scarano FR (2010) Normas jurídicas para a restauração ecológica: uma barreira a mais a dificultar o êxito das iniciativas? Revista Árvore 34(3):471–485. https://doi.org/10.1590/S0100-67622010000300011

Durigan G, Engel VL (2015) Chapter 2 - Restauração de ecossistemas no Brasil: onde estamos e para onde podemos ir? In: Martins SV (ed), Restauração ecológica de ecossistemas degradados (2nd ed.). Editora UFV, Viçosa, Brazil, pp 42–69.

Durigan G, Guerin N, Costa JNMN (2013) Ecological restoration of Xingu Basin headwaters: motivations, engagement, challenges and perspectives. Philos Trans R Soc B 368:20120165. http://dx.doi.org/10.1098/rstb.2012.0165

Emer C, Galetti M, Pizo MA, Guimarães PR, Moraes S, Piratelli A, Jordano P (2018) Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. Ecol Lett 21(4):484–493. https://doi.org/10.1111/ele.12909

Engel VL (2011) Princípios silviculturais aplicados à restauração ecológica. Ação Ambiental 14(45):7–9.

Engel VL, Martins FR (2005) Reproductive phenology of Atlantic Forest tree species in Brazil: an eleven year study. Trop Ecol 46(1):1–16.

Engel VL, Massoca PES, Patricio AL, Munhoz MO (2002) Implantação de espécies nativas em solos degradados através de semeadura direta. In: Balensiefer M (ed.), Proceedings of V Simpósio Nacional Sobre Recuperação de Áreas Degradadas-2002: Água e Biodiversidade. Anais, SOBRADE, Curitiba, Brazil, pp 407–409.

Engel VL, Parrotta JA (2001) An evaluation of direct seeding for reforestation of degraded lands in central São Paulo state, Brazil. For Ecol Manag 152(1):169–181. https://doi.org/10.1016/s0378-1127(00)00600-9

Escobar DFE, Silveira FAO, Morellato LPC (2018) Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality. Ann Bot 121(6):1197–1209. https://doi.org/10.1093/aob/mcy006

Feltran-Barbieri R, Féres JG (2021) Degraded pastures in Brazil: improving livestock production and forest restoration. R Soc Open Sci 8:201854. https://doi.org/10.1098/rsos.201854

Ferragutti AC (2021) Padrões espaço-temporais de dispersão de sementes de espécies arbóreas úteis para a restauração ecológica na região de transição Cerrado-Amazônia. MSc Dissertation, Universidade do Estados do Mato Grosso, Nova Xavantina, Brazil. 64 pp.

Ferraz IDK, Camargo JLC, Mesquita MR, Santos BA, Brum HD, Albuquerque MCF (2019) Guide to Amazonian: fruits, seeds & seedlings. Editora do INPA, Manaus, Brazil.

Ferreira BZ, Garcia JM, Torezan JMD, Durigan G (2013) Chapter 6 - Controle de formigas cortadeiras em plantios de restauração. In: Durigan G, Ramos VS (eds) Manejo adaptativo: primeiras experiências na restauração de ecossistemas. Páginas e Letras Editora & Gráfica Ltda., São Paulo, Brazil, pp 9–13.

Ferreira MC, Cordeiro AOO, Sampaio AB, Schmidt IB, Vieira DLM (2023) Direct seeding versus seedling planting: survival, biomass, growth, and cost up to 6 years for four tropical seasonal tree species. Restor Ecol 31(4):e13807. https://doi.org/10.1111/rec.13807

Ferreira MC, Vieira DLM, Malta Filho E, Rocha G, Miranda E, Antoniazzi L, Basso I (2020) Protocolo padrão de avaliação e manejo adaptativo para novos plantios com semeadura direta. Iniciativa Caminhos da Semente/Agroicone/Embrapa/ISA, Brasília, Brazil.

Ferreira MC, Vieira DLM (2024) Making the most of native seeds: management techniques interact with seed and seedling traits for enhancing direct seeding success. For Ecol Manag 574:122353. https://doi.org/10.1016/j.foreco.2024.122353

Ferreira RA, Davide AC, Bearzoti E, Souza MM (2007) Semeadura direta com espécies arbóreas para recuperação de ecossistemas florestais. Cerne 13(3):271–279.

Freire JM, Piña-Rodrigues FCM, Lima ER, Sodré SRC, Corrêa RX (2007) Estrutura genética de populações de *Schizolobium parahyba* (Vell.) Blake (guapuruvu) por meio de marcadores RAPD. Scientia Forestalis 74:27–35.

Freitas MG, Rodrigues SB, Campos-Filho EM, Carmo GHP, Veiga JM, Junqueira RGP, Vieira DLM (2019) Evaluating the success of direct seeding for tropical forest restoration over ten years. For Ecol Manag 438:224–232. https://doi.org/10.1016/j.foreco.2019.02.024

Frigieri FF, Iwanicki NS, Gandara FB, Ferraz EM, Romão GO, Coletti GF, Souza VC, Moreno MA (2016) Guia de plântulas e sementes da Mata Atlântica do estado de São Paulo. IPEF, Piracicaba, SP, Brazil.

Garcia IP, Forti LC, Engel VL, Andrade APP, Wilcken CF (2003) Ecological interaction between *Atta sexdens* (Hymenoptera: Formicidae) and the vegetation of a mesophyll semideciduous forest fragment in Botucatu, SP, Brazil. Sociobiology 42(2):265–283.

Garcia JM, Bordignon AM, Gonzaga GS, Torezan JMD (2020) Tree seedling responses to leaf-cutting ants herbivory in Atlantic Forest restoration sites. Biotropica 52(5):884–895. https://doi.org/10.1111/btp.12808

Garcia LC, Hobbs RJ, Ribeiro DB, Tamachiro JY, Santos FAM, Rodrigues RR (2016) Restoration over time: is it possible to restore trees and non-trees in high-diversity forests? Appl Veg Sci 19:656–666. https://doi.org/10.1111/avsc.12264

Giacomini IF (2016) Técnicas de restauração ecológica em nascentes e matas ciliares, Itaara, RS. PhD Dissertation, Universidade Federal de Santa Maria, Santa Maria, Brazil. 89 pp.

Guerin N, Isernhagen I, Vieira DLM, Malta Filho EC, Campos RJB (2015) Chapter 11 - Avanços e próximos desafios da semeadura direta para a restauração ecológica. In: Martins SV (ed) Restauração ecológica de ecossistemas degradados (2nd ed.). Editora UFV, Viçosa, Brazil, pp 331–376.

Guerra A, Reis LK, Borges FLG, Ojeda PTA, Pineda DAM, Miranda CO, Maidana DPFL, Santos TMR, Shibuya PS, Marques MCM, Laurance SGW, Garcia LC (2020) Ecological restoration in Brazilian biomes: identifying advances and gaps. For Ecol Manag 458:117802. https://doi.org/10.1016/J.FORECO.2019.117802

Hamrick JL, Loveless MD (1986) Isozyme variation in tropical trees: procedures and preliminary results. Biotropica 18:201–207. https://doi.org/10.2307/2388485

Harris B (2020) Brazil pays a high price for its mining industry. The Financial Times, Dec 2020. https://www.ft.com/content/2a393038-0cdb-4401-8fad-23439d6d72ea (last accessed 10 July 2024).

Holl K, Reid JL, Cole RJ, Oviedo F, Rosales JA, Zahawi R (2020) Applied nucleation facilitates tropical forest recovery: lessons learned from a 15-year study. J Appl Ecol 57(12):2316–2328. https://doi.org/10.1111/1365-2664.13684

Howe F, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol System 3:201–228. https://doi.org/10.1146/ANNUREV.ES.13.110182.001221

IBGE (2012) Manual técnico da vegetação Brasileira (2nd ed.). Instituto Brasileiro de Geografia e Estatística-IBGE, Rio de Janeiro, Brazil (Manuais Técnicos em Geociências, 1).

https://biblioteca.ibge.gov.br/index.php/biblioteca-catalogo?view=detalhes&id=263011 (last accessed 3 June 2025).

IBGE (2024) Biomas e Sistema Costeiro-Marinho do Brasil 2024. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, BR. https://www.ibge.gov.br/apps/biomas/#/home/ (last accessed 27 July 2024).

Jalonen R, Valette M, Boshier D, Duminil J, Thomas E (2018) Forest and landscape restoration severely constrained by a lack of attention to the quantity and quality of tree seed: Insights from a global survey. Conserv Lett 11(4):e12424. https://doi.org/10.1111/conl.12424

JBRJ (2024) Flora e Funga do Brasil. Programa Reflora/CNPq, Jardim Botânico do Rio de Janeiro. https://floradobrasil.jbrj.gov.br (last accessed 7 August 2024)

Jordano P, Garcia C, Godoy JA, García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. PNAS 104(9):3278–3282. https://doi.org/10.1073/PNAS.0606793104

Kitajima K, Fenner M (2000) Chapter 16 - Ecology of seedling regeneration. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, 2nd ed, CABI Publisher, Wallingford, UK, pp 331–359.

Knowles OH, Parrotta JA (1995) Amazonian forest restoration: an innovative system for native species selection based on phenological data and field performance indices. Commonwealth For Rev 74(3): 230:243.

Knowles OH, Parrotta JA (1997) Phenological observations and tree seed characteristics in an Equatorial Moist Forest at Trombetas, Para State, Brazil. In: Lieth H, Schartz MD (eds) Phenology in seasonal climates I. Blackwell Publishers, Leiden, The Netherlands, pp 67–84.

Laumann PD, Ferreira MC, Silva DA, Vieira DLM (2023) Germination traits explain the success of direct seeding restoration in the seasonal tropics of Brazil. For Ecol Manag 529:120706. https://doi.org/10.1016/j.foreco.2022.120706

Leão BM, Braga MA, Pereira IM, Santos GC (2022) Ecological restoration in pasture areas with direct seeding. Ciencia Florestal 32(4):1928–1947. https://doi.org/10.5902/1980509863831

Liaffa ABS (2020) Restauração ecológica no Cerrado: intenso preparo de solo e alta densidade de semeadura não eliminam a necessidade de erradicação de gramíneas exóticas invasoras. MSc Dissertation, Universidade de Brasília, Brasília, Brazil. 64 pp.

Lima RAF, Dauby G, Gasper AL, Fernandez EP, Vibrans AC, Oliveira AA, Prado PI, Souza VC, Siqueira MF, Ter Steege H (2024) Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. Science 383(6679):219–225. https://doi.org/10.1126/science.abq5099

Lima RAF, Oliveira AA, Pitta GR, Gasper AL, Vibrans AC, Chave J, Ter Steege H, Prado PI (2020) The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. Nat Commun 11(1):1–16. https://doi.org/10.1038/s41467-020-20217-w

Lima VVF, Vieira DLM, Sevilha AC, Salomão AN (2008) Germinação de espécies arbóreas de floresta estacional decidual do vale do rio Paranã em Goiás após três tipos de armazenamento por até 15 meses. Biota Neotropica 8(3):89–97. https://doi.org/10.1590/s1676-06032008000300008

Magalhães MLL (2017) Germinação e estabelecimento de arbustos e árvores pioneiros para a restauração florestal por semeadura direta. MSc Dissertation, Universidade de Brasília, Brasília, Brazil. 68 pp.

Malavasi UC, Gasparino D, Malavasi MM (2005) Semeadura direta na recomposição vegetal de áreas ciliares: efeitos da sazonalidade, uso do solo, exclusão da predação, e profundidade na sobrevivência inicial. Semina: Ciências Agrárias 26(4):449-454.

Malavasi UC, Klein J, Malavasi MM (2010) Efeito de um protetor físico na semeadura direta de duas espécies florestais em área de domínio ciliar. Revista Árvore 34(5):781–787. https://doi.org/10.1590/s0100-67622010000500003

MapBiomas (2023) As florestas do Brasil 1985–2022. In: Projeto MapBiomas, mapeamento anual de cobertura e uso da terra no Brasil entre 1985 a 2022 – Coleção 8. https://brasil.MapBiomas .org/wp-content/uploads/sites/4/2023/09/FACT_port-versao-final.pdf (last accessed 4 April 2025).

Martins AM (2009) O processo de regeneração natural e a restauração de ecossistemas em antigas áreas de produção florestal. MSc Dissertation, Universidade de São Paulo, Piracicaba, Brazil. 89 pp. https://doi.org/10.11606/D.11.2009.tde-18052009-150204

Masuthi D, Barad A, Mori RB (2023) Chapter 14 - Conserving biodiversity: native seeds in ecological seed science and technology. In: Chaturvedi R, Chacko A, Polara M, Panda D (eds) Seed science and technology. Unraveling the secrets of plant propagation. Elite Publishing House, New Delhi, India, pp 199–223.

Meli P, Isernhagen I, Brancalion PHS, Isernhagen ECC, Behling M, Rodrigues RR (2018) Optimizing seeding density of fast-growing native trees for restoring the Brazilian Atlantic Forest. Restor Ecol 26(2):212–219. https://doi.org/10.1111/rec.12567

Mijnsbrugge KV, Bischoff A, Smith B (2010) A question of origin: where and how to collect seed for ecological restoration. Basic Appl Ecol 11(4):300–311. https://doi.org/10.1016/j.baae.2009.09.002

Miranda Neto A, Martins SV, Silva KA, Gleriani JM (2012) Florística e estrutura do estrato arbustivo-arbóreo de uma floresta restaurada com 40 anos, Viçosa, MG. Revista Árvore 36:869–878. https://doi.org/10.1590/S0100-67622012000500009

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Chapter 1 - Global biodiversity conservation: the critical role of hotspots. In: Zachos F, Habel J (eds) Biodiversity hotspots. Springer, Berlin, Germany. pp 3–22. https://doi.org/10.1007/978-3-642-20992-5_1

Moraes MLT, Kageyama PY, Sebbenn AM (2005) Diversidade e estrutura genética espacial em duas populações de *Myracrodruon urundeuva* Fr. All. sob diferentes condições antrópicas. Revista Árvore 29(2):281–289.

Mori ES, Piña-Rodrigues FCM, Freitas NP (2012) Sementes florestais: guia para germinação de 100 espécies nativas. Instituto Refloresta, São Paulo, Brazil.

NEMA/UNIVASF (2022) Projeto RE-Habitar Ararinha-azul: coleta, beneficiamento e armazenamento de sementes nativas da Caatinga. Núcleo de Ecologia e Monitoramento Ambiental, Petrolina, Brazil.

NEMA/UNIVASF (2023) Projeto Re-Habitar Ararinha-azul Vol. 5:Implantação de técnicas para a recuperação de áreas degradadas. Núcleo de Ecologia e Monitoramento Ambiental, Petrolina, Brazil.

Oliveira AS (2013) Semeadura direta e plantio de mudas para recuperação de nascentes no rio Piauitinga-SE. MSc Dissertation, Universidade Federal de Sergipe, São Cristóvão, Brazil. 58 pp.

Oliveira AS, Trindade ALC, Clemente CC, Cho DF, Morelli F, Zacharias GC, Ferreira GP, Morita JP, Caitano LL, Muchagata M, Oliveira MS, Mattos PP, Ferraz PC, Leão RA, Oliveira YMM (2022) Florestas. In: Brasil/Ministério do Meio Ambiente. Relatório de qualidade do meio ambiente: RQMA: Brasil 2020, pp 302–356.

Oliveira MC, Leite JB, Galdino OPS, Ogata RS, Silva DA, Ribeiro JF (2019) Sobrevivência e crescimento de espécies nativas do Cerrado após semeadura direta na recuperação de pastagem abandonada. Neotrop Biol Conserv 14(3):313–327. https://doi.org/10.3897/neotropical.14.e38290

Oliveira PE (2008) Chapter 9 - Fenologia e biologia reprodutiva das espécies de Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: Ecologia e flora, v.1. EMBRAPA Informação Tecnológica, Brasília, Brazil, pp 274–290.

Oliveira TGS, Rodrigues AG, Souza PP, Ribeiro LM (2013) Uso de fitorreguladores na superação da dormência em sementes de macaúba. Acta Scientiarum - Agronomy 35(4):505–511. https://doi.org/10.4025/actasciagron.v35i4.16385

Padovezi A, Adams C, Chazdon RL, Mendonça MA, Secco L, Campos-Filho EM, Sampaio A, Damasceno E, Albuquerque N, Santarem F, Camargo ME, Pinã-Rodrigues FM (2024) Native seed collector networks in Brazil: sowing social innovations for transformative change. People Nat 6(5):1905–1921. https://doi.org/10.1002/pan3.10692

Parrotta JA, Knowles OH (2001) Restoring tropical forests on lands mined for bauxite: examples from the Brazilian Amazon. Ecol Eng 17(2–3):219–239. https://doi.org/10.1016/S0925-8574(00)00141-5

Parrotta JA, Knowles OH, Wunderle Jr JM (1997) Development of floristic diversity in 10-year-old restoration forests on a bauxite mined site in Amazonia. For Ecol Manag 99(1–2):21–42. https://doi.org/10.1016/S0378-1127(97)00192-8

Parrotta JA, Knowles OH (1999) Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restor Ecol 7(2):103–116. https://doi.org/10.1046/j.1526-100X.1999.72001.x

Parrotta JA, Turnbull JW, Jones N (1997) Catalyzing native forest regeneration on degraded tropical lands.

For Ecol Manag 99(1–2):1–7. https://doi.org/10.1016/S0378-1127(97)00190-4

Passaretti RA, Pilon NAL, Durigan G (2020) Weed control, large seeds and deep roots: drivers of success in direct seeding for savanna restoration. Appl Veg Sci 23(3):406–416. https://doi.org/10.1111/avsc.12495

Pedrini S, Dixon KW (2020) International principles and standards for native seeds in ecological restoration. Restor Ecol 28(S3):S286–S303. https://doi.org/10.1111/rec.13155

Pedrini S, Gibson-Roy P, Trivedi C, Gálvez-Ramírez C, Hardwick K, Shaw N, Frischie S, Laverack G, Dixon K (2020) Collection and production of native seeds for ecological restoration. Restor Ecol 28(S3):S228–S238. https://doi.org/10.1111/rec.13190

Pellizzaro KF, Cordeiro AOO, Alves M, Motta CP, Rezende GM, Silva RRP, Ribeiro JF, Sampaio AB, Vieira DLM, Schmidt IB (2017) “Cerrado” restoration by direct seeding: field establishment and initial growth of 75 trees, shrubs and grass species. Braz J Bot 40(3):681–693. https://doi.org/10.1007/s40415-017-0371-6

Pereira SR, Laura VA, Souza ALT (2013) Establishment of Fabaceae tree species in a tropical pasture: influence of seed size and weeding methods. Restor Ecol 21(1):67–74. https://doi.org/10.1111/j.1526-100X.2011.00858.x

Pereira JR (2021) Métodos de controle de formigas cortadeiras em sistemas orgânicos de produção: uma revisão. Revista Ambientale 13(4):10–24. https://doi.org/10.48180/ambientale.v13i4.318

Pieruzzi FP (2022) Chapter 12 - O paradigma da ortodoxia x recalcitrância e a conservação de sementes nativas. In: Albuquerque NCB et al. (eds) Sementes Florestais da Mata Atlântica: um Guia Para o Manejo de Espécies da Hileia Baiana. Programa Arboretum de Conservação e Restauração da Diversidade Florestal, Teixeira de Freitas, Brazil, pp 87–103.

Piña-Rodrigues FCM, Balistiero MF (2015) Sementes Florestais Tropicais: da ecologia à produção. ABRATES, Londrina, Brazil.

Piña-Rodrigues FCM, Freire JM, Leles PSS, Breir PSS (2007) Parâmetros técnicos para produção de sementes florestais. EDUR/UFRRJ, Seropédica, Brazil.

Pires MM, Galetti M (2023) Beyond the “empty forest”: The defaunation syndromes of neotropical forests in the Anthropocene. Glob Ecol Conserv 41:e02362. https://doi.org/10.1016/j.gecco.2022.e02362

Pivello VR (2011) The use of fire in the Cerrado and Amazonian rainforests of Brazil: past and present. Fire Ecol 7:24–39. https://doi.org/10.4996/fireecology.0701024

Ressel K, Guilherme FAG, Schiavini I, Oliveira PE (2004) Ecologia morfofuncional de plântulas de espécies arbóreas da Estação Ecológica do Panga, Uberlândia, Minas Gerais. Revista Brasileira de Botânica 27:311–323.

Raupp PP, Ferreira MC, Alves M, Campos-Filho EM, Sartorelli AR, Consolaro HN, Vieira DLM (2020) Direct seeding reduces the costs of tree planting for forest and savanna restoration. Ecol Eng 148:105788. https://doi.org/10.1016/j.ecoleng.2020.105788

Redário/CTSF (2023) Desafios e oportunidades para o desenvolvimento da cadeia produtiva de sementes nativas para a restauração de ecossistemas no Brasil (Nota Técnica 1). https://redario.org.br/nota-tecnica (last accessed 10 August 2024).

Redário (2024) Tributação da cadeia produtiva de sementes nativas para a restauração de ecossistemas no Brasil. Nota Técnica. https://redario-site.terrakrya.com/biblioteca?tag&category&search&type&language&media=66cf2f92079ae12bffee5c27 (last accessed 10 August 2024).

Reis LK, Guerra A, Colado MLZ, Borges FLG, Oliveira MR, Gondim EX, Sinani TRF, Guerin N, Garcia LC (2019) Which spatial arrangement of green manure is able to reduce herbivory and invasion of exotic grasses in native species? Ecol Appl 29(8):e02000. https://doi.org/10.1002/eap.2000

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142(6):1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Ribeiro JF, Kuhlmann M, Ogata RS, Oliveira MC, Vieira DLM, Sampaio AB (2022) Guia de plantas do cerrado para recomposição da vegetação nativa, 2nd ed, Embrapa, Brasília, DF, Brazil.

Ribeiro JF, Walter BMT (2008) Chapter 7 - As principais fitofisionomias do cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: ecologia e flora, v.1. EMBRAPA Informação Tecnológica, Brasília, Brazil, pp 152–212.

Rocha GB, Basso IY, Vieira DLM, Antoniazzi LB, Santos TR (2020a) Direct seeding for restoration. Miscellaneous experiences in Brazil. Agroícone, São Paulo, Brazil. https://www.agroicone.com.br/wp-content/uploads/2021/01/Direct-seeding-restoration-experiences-in-Brazil_2020.pdf (last accessed 10 July 2024).

Rocha GB, Vieira DLM, Campos-Filho EM, Ferreira MC, Miranda E, Alves M, Sampaio A, Antoniazzi L (2020b) Guia de semeadura direta para restauração de florestas e cerrados, 1a ed, Agroicone Ltda (Caminhos da Semente), São Paulo, Brazil.

Rodrigues SB, Freitas MG, Campos-Filho EM, Carmo GHP, Veiga JM, Junqueira RGP, Vieira DLM (2019) Direct seeded and colonizing species guarantee successful early restoration of South Amazon forests. For Ecol Manag 451:e117559. https://doi.org/10.1016/j.foreco.2019.117559

Ruiz-Jaen MC, Aide TM (2005) Restoration success: how is it being measured? Restor Ecol 13(3):569–577. https://doi.org/10.1111/j.1526-100X.2005.00072.x

Salazar A, Goldstein G, Franco AC, Miralles-Wilhelm F (2011) Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas. Seed Sci Res 21(2):103–116. https://doi.org/10.1017/S0960258510000413

Sampaio AB, Holl KD, Scariot A (2007) Does restoration enhance regeneration of seasonal deciduous forests in pastures in central Brazil? Restor Ecol 15(3):462–471. https://doi.org/10.1111/j.1526-100X.2007.00242.x

Sampaio AB, Vieira DLM, Cordeiro AODO, Aquino FDG, Sousa ADP, Albuquerque LB, Schmidt IB, Ribeiro JF, Pellizaro KF, Sousa FS, Moreira AG, Santos ABP, Rezende GM, Silva RRP, Alves M, Motta CP, Oliveira MC, Cortes CDA, Ogata R (2015) Guia de restauração do Cerrado. Volume 1 - semeadura direta. Universidade de Brasília/Rede de Sementes do Cerrado, Brasília, Brazil.

Santos LCA (2010) A eficiência da semeadura direta para a revegetação de uma jazida de cascalho na Fazenda Água Limpa, APA Gama Cabeça de Veado, Brasília, DF. MSc Dissertation, Universidade de Brasília, Brasília, Brazil. 106 pp.

Schmidt IB, Urzedo DI, Piña-Rodrigues FCM, Vieira DLM, Rezende GM, Sampaio AB, Junqueira RGP (2019) Community-based native seed production for restoration in Brazil – the role of science and policy. Plant Biol 21(3):389–397. https://doi.org/10.1111/PLB.12842

Schmidt L (2000) Guide to Handling of Tropical and Subtropical Forest Seed, 1st ed, Danida Forest Tree Centre, Humleback, Denmark.

Silva APM, Schweizer D, Marques HR, Teixeira AMC, Santos TVMN, Sambuichi RHR, Badari CG, Gaudare U, Brancalion PHS (2017) Can current native tree seedling production and infrastructure meet an increasing forest restoration demand in Brazil? Restor Ecol 25(4):509–515. https://doi.org/10.1111/rec.12470

Silva KB, Reiniger LRS, Serrote CML, Rabaiolli SMS, Stefenon VM, Costa LS, Ziegler ACF (2021) Variabilidade genética de fragmentos naturais de *Luehea divaricata* Mart. & Zucc. no bioma Mata Atlântica. Biodiversidade Brasileira 11(4):4–11. https://doi.org/10.37002/biobrasil.v11i4.1837

Silva MC, Moonlight P, Oliveira RS, Rowland L, Pennington RT (2025) COSST: a tool to facilitate seed provenancing for climate-smart ecosystem restoration. J Appl Ecol 62(3):677–688. https://doi.org/10.1111/1365-2664.14854

Silva Neto ACSR, Marques R, Ribeiro Júnior NG, Veiga JB, Caioni C, Claudino WV (2020) Planting of seedlings and direct seeding with different inputs in pioneer species in the southeastern amazon. Floresta e Ambiente 27(2):e20190084. https://doi.org/10.1590/2179-8087.008419

Silva RRP, Oliveira DR, Rocha GPE, Vieira DLM (2015) Direct seeding of Brazilian savanna trees: effects of plant cover and fertilization on seedling establishment and growth. Restor Ecol 23(4):393–401. https://doi.org/10.1111/REC.12213

Silva RRP, Vieira DLM (2017) Direct seeding of 16 Brazilian savanna trees: responses to seed burial, mulching and an invasive grass. Appl Veg Sci 20(3):410–421. https://doi.org/10.1111/avsc.12305

Silva TD (2019) Aceleração do processo de restauração de florestas tropicais através do uso de cobertura transitória ou poda. MSc Dissertation, Universidade de São Paulo, Piracicaba, Brazil. 86 pp. https://doi.org/10.11606/D.11.2019.tde-22072019-103011

Soares-Filho B, Rajão R, Macedo M, Carneiro A, Costa W, Coe M, Rodrigues H, Alencar A (2014) Cracking Brazil's forest code. Science 344(6182):363–364. https://doi.org/10.1126/science.1246663

Sonter LJ, Herrera D, Barrett DJ, Galford GL, Moran CJ, Soares-Filho BS (2017) Mining drives extensive deforestation in the Brazilian Amazon. Nat Commun 8(1):1–7. https://doi.org/10.1038/s41467-017-00557-w

SOS Mata Atlântica/INPE (2023) Atlas dos remanescentes florestais da Mata Atlântica período 2021–2022. Relatório Técnico. SOS Mata Atlântica, São Paulo, Brazil. https://cms.sosma.org.br/wp-content/uploads/2023/05/SOSMAAtlas-da-Mata-Atlantica_2021-2022-1.pdf (last accessed 12 January 2025).

Souza CR, Souza FC, Françoso RD, Maia VA, Pinto JRR, Higuchi P, Silva AC, Prado Júnior JA, Farrapo CL, Lenza E, Mews H, Rocha HLL, Mota SL, Rodrigues ALC, Silva-Sene AM, Moura DM, Araújo FC, Oliveira F, Gianasi FM, Santos RM (2024) Functional and structural attributes of Brazilian tropical and subtropical forests and savannas. For Ecol Manag 558:121811. https://doi.org/10.1016/j.foreco.2024.121811

Souza DC (2022) Forest restoration by direct seeding: a global bibliometric analysis. Restor Ecol 30(8):1–9. https://doi.org/10.1111/rec.13631

Souza DC (2023) Avanços, desafios e diretrizes para a restauração ecológica por semeadura direta de espécies arbóreas. PhD Dissertation, Universidade Estadual Paulista "Júlio de Mesquita Filho, Botucatu, Brazil. 171 pp.

Souza DC, Engel VL (2017) Pre-emergence herbicides affect seedling emergence of tropical forest tree species. J For Res 28(4):733–739. https://doi.org/10.1007/s11676-016-0348-5

Souza DC, Engel VL (2018) Direct seeding reduces costs, but it is not promising for restoring tropical seasonal forests. Ecol Eng 116:35–44. https://doi.org/10.1016/j.ecoleng.2018.02.019

Souza DC, Engel VL (2023) Advances, challenges, and directions for ecological restoration by direct seeding of trees: lessons from Brazil. Biol Conserv 284:110172. https://doi.org/10.1016/j.biocon.2023.110172

Souza DC, Engel VL (2024) Seed functional traits as predictors of seedling establishment success in Brazilian tropical forest restoration. Biotropica 56(4):e13355. https://doi.org/10.1111/btp.13355

Souza DC, Engel VL, Mattos EC (2021) Direct seeding to restore tropical seasonal forests: effects of green manure and hydrogel amendment on tree species performances and weed infestation. Restor Ecol 29(1):1–7. https://doi.org/10.1111/rec.13277

Souza ECA, Silva FM, Francisco BS, Dutra FB, Piña-Rodrigues FCM, Piotrowski I (2024) Regularização da colheita de sementes em unidades de conservação. Caderno Pedagógico 21(9):e7520. https://doi.org/10.54033/cadpedv21n9-040

Souza Jr CM, Shimbo JZ, Rosa MR, Parente LL, Alencar AA, Rudorff BFT, Hasenack H, Matsumoto M, Ferreira LG, Souza-Filho PWM, Oliveira SW, Rocha WF, Fonseca AV, Marques CB, Diniz CG, Costa D, Monteiro D, Rosa ER, Vélez-Martin E, Azevedo T (2020) Reconstructing three decades of land use and land cover changes in Brazilian biomes with Landsat archive and earth engine. Remote Sens 12(17):2735. https://doi.org/10.3390/RS12172735

Souza Jr CN, Brancalion PHS (2016) Sementes e mudas. Guia para propagação de árvores brasileiras. Oficina de Textos, São Paulo, Brazil.

Strassburg BBN, Latawiec AE, Barioni LG, Nobre CA, Silva VP, Valentim JF, Vianna M, Assad ED (2014) When enough should be enough: improving the use of current agricultural lands could meet production demands and spare natural habitats in Brazil. Glob Environ Chang 28(1):84–97. https://doi.org/10.1016/j.gloenvcha.2014.06.001

Suganuma MS, Durigan G (2015) Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. Restor Ecol 23:238–251. https://doi.org/10.1111/rec.12168

Ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomão RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE, Molino JF, Monteagudo A, Vargas PN, Montero JC, Feldpausch TR, Coronado

ENH, Killeen TJ, Mostacedo B, Vasquez R, Assis RL, Silman MR (2013) Hyperdominance in the Amazonian tree flora. Science 342(6156):1243092. https://doi.org/10.1126/science.1243092

Thomas E, Jalonen R, Loo J, Boshier D, Gallo L, Cavers S, Bordács S, Smith P, Bozzano M (2014) Genetic considerations in ecosystem restoration using native tree species. For Ecol Manag 333:66–75. https://doi.org/10.1016/j.foreco.2014.07.015

Tunjai P, Elliott S (2012) Effects of seed traits on the success of direct seeding for restoring southern Thailand's lowland evergreen forest ecosystem. New For 43:319–333. https://doi.org/10.1007/s11056-011-9283-7

Urzedo DI, Fisher R, Piña-Rodrigues FCM, Freire JM, Junqueira RGP (2019) How policies constrain native seed supply for restoration in Brazil. Restor Ecol 27(4):768–774. https://doi.org/10.1111/rec.12936

Urzedo DI, Piña-Rodrigues FCM, Feltran-Barbieri R, Junqueira RGP, Fisher R (2020) Seed networks for upscaling forest landscape restoration: is it possible to expand native plant sources in Brazil? Forests 11(3):259. https://doi.org/10.3390/F11030259

Vaz Ferreira A, Bruna EM, Vasconcelos HL (2011) Seed predators limit plant recruitment in Neotropical savannas. Oikos 120(7):1013–1022. https://doi.org/10.1111/J.1600-0706.2010.19052.X

Vencovsky R (1987) Tamanho efetivo populacional na coleta e preservação de germoplasma de espécies alógamas. Ipef 35:79–84.

Viani RAG, Barreto TE, Farah FT, Rodrigues RR, Brancalion PHS (2018) Monitoring young tropical forest restoration sites: how much to measure? Trop Conserv Sci 11:1–9. https://doi.org/10.1177/1940082918780916

Villota-Cerón DE (2020) Remoção de sementes e herbivoria de mudas em diferentes sistemas de restauração ecológica da Floresta Estacional Semidecidual. PhD Dissertation, Universidade Estadual Paulista, Botucatu, Brazil. 103 pp.

Villota-Cerón DE, Engel VL (2021) Similarity in seed removal patterns of four tree species in active and passive restoration treatments of the tropical seasonal forest after 23 years. For Ecol Manag 499:119608. https://doi.org/10.1016/j.foreco.2021.119608

Vozzo JE (ed) (2002) Tropical tree seed manual. USDA Forest Service, Agriculture Handbook 721, Washington D.C., USA.

Zambrano IAN (2017) Caracterização ecológica de sementes e plântulas de árvores de cerrado. MSc Dissertation, Universidade de Brasília, Brasília, Brazil. 59 pp.

Appendix 1. List of species evaluated in seeding field trials in Brazil, in order of decreasing establishment percentage (Source: Souza (2023)).

Species	Family	Functional traits[e]											E%[f]	Biome[g]	Forest type[g]
		GR	DS	SM[a]	SH[b]	SW[c]	GS[d]	ST	PC		EC	FC	SD		
Aspidosperma macrocarpon Mart. & Zucc.	Apocynaceae	Sl	Wi	1.43	Ro	8.3	25.0	Or	Ep	Ph	Ph	No	40.35	CE	FS
Cassia grandis L. f.	Fabaceae	Fa	Se	0.53	Ov	16.2	34.0	Or	Ep	Ph	St	Yes	38.80	AM, CE, AF, PT	GF, UAF, SSF, DR
Sapindus saponaria L.	Sapindaceae	Sl	An	3.85	Ro	17.0	30.0	Or	Hy	Cr	St	No	35.06	AM, CE, AF, PT	GF, UAF, SSF, DR
Magonia pubescens A. St.-Hil.	Sapindaceae	Sl	Wi	2.22	Ro	9.6	27.5	Or	Hy	Ph	St	No	34.55	AM, CA, CE	FS, SSF
Mabea fistulifera Mart.	Euphorbiaceae	Fa	Se	0.09	Fl	6.5	25.5	Or	Ep	Ph	Ph	No	34.45	AM, CA, CE, AF	FS, GF, UAF, SDF, DR, AF
Enterolobium gummiferum (Mart.) J. F. Macbr.	Fabaceae	Sl	An	0.51	Fl	9.9	10.5	Or	Ep	Ph	St	Yes	33.78	AM, CE	FS
Hymenaea stigonocarpa Mart.	Fabaceae	Fa	An	4.00	Fl	11.8	34.5	Or	Ep	Ph	St	Yes	32.05	AM, CA, CE, PT	FS, SSF
Hymenaea courbaril L.	Fabaceae	Sl	An	5.07	Fl	11.4	36.0	Or	Ep	Ph	St	Yes	25.85	AM, CA, CE, AF, PT	FS, GF, UAF, DR
Eugenia uniflora L.	Myrtaceae	Sl	An	0.44	Fl	50.0	26.0	Re	Hy	Cr	St	No	25.80	CA, CE, AF, PA	FS, GF, SEF, SSF, DR, AF
Qualea grandiflora Mart.	Vochysiaceae	Sl	Wi	0.19	Ro	10.4	28.0	Re	Ep	Ph	Ph	No	24.22	AM, CA, CE, AF, PT	FS
Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S. Moore	Bignoniaceae	Sl	Wi	0.16	Ro	2.9	11.0	Or	Hy	Ph	St	No	21.56	AM, CA, CE, AF, PT	FS, SDF, DR
Dipteryx alata Vogel	Fabaceae	Fa	An	1.22	Fl	6.3	25.0	Or	Ep	Ph	St	Yes	21.32	CE	FS, GF, SSF
Eugenia dysenterica (Mart.) DC.	Myrtaceae	Sl	An	0.67	Fl	33.2	22.5	Re	Hy	Cr	St	No	21.30	CA, CE, AF	FS
Enterolobium contosrtisiliquum (Vell.) Morong	Fabaceae	Fa	An	0.19	Fl	5.8	32.0	Or	Ep	Ph	St	Yes	20.90	CA, CE, AF, PA, PT	FS, GF, SSF, DR
Copaifera langsdorffii Desf.	Fabaceae	Sl	An	0.47	Fl	8.1	36.0	Or	Ep	Ph	St	Yes	20.88	AM, CA, CE, AF	FS, GF, UAF, SSF, DR
Handroanthus serratifolius (Vahl) S. Grose	Bignoniaceae	Sl	Wi	0.04	Ro	5.7	19.0	Or	Hy	Ph	St	No	20.87	AM, CA, CE, AF, PT	UAF, SEF, DR, AF
Kielmeyera coriacea Mart. & Zucc.	Calophyllaceae	Sl	Wi	0.06	Ro	6.9	37.5	Or	Ep	Ph	Ph	No	18.98	AM, CE	FS
Libidibia ferrea (Mart. ex. Tul.) L. P. Queiroz	Fabaceae	Sl	Wi	0.02	Fl	8.6	37.5	Or	Ep	Ph	Ph	Yes	16.89	CA, CE, AF	GF, SDF, SSF, DRF
Ceiba speciosa (A. St.-Hil.) Ravenna	Malvaceae	Sl	Wi	0.14	Ov	16.6	19.0	Or	Ep	Ph	Ph	No	16.58	AM, CA, CE, AF, PA, PT	SSF, DR
Brosimum gaudichaudii Trécul	Moraceae	Sl	An	0.02	Fl	45.8	35.0	Or	Hy	Cr	St	No	15.07	AM, CA, CE, AF	FS
Peltophorum dubium (Spreng.) Taub.	Fabaceae	Fa	Wi	0.05	Ov	13.3	33.0	Or	Ep	Ph	Ph	Yes	14.42	CA, CE, AF, PT	FS, GF, SDF, SSF, DRF, AF
Vatairea macrocarpa (Benth.) Ducke	Fabaceae	Sl	Wi	1.43	Ov	6.6	28.0	Or	Hy	Ph	St	Yes	14.16	AM, CA, CE	FS

Appendix 1. (continued)

Species	Family	Functional traits[e]											E%[f]	Biome[g]	Forest type[g]
		GR	DS	SM[a]	SH[b]	SW[c]	GS[d]	ST	PC		EC	FC	SD		
Senna alata (L.) Roxb.	Fabaceae	Fa	Se	0.03	Ov	7.8	30.0	Or	Ep	Ph	Ph	No	12.90	AM, CA, CE, AF, PT	FS, UAF, SSF, DR, AF
Cedrela fissilis Vell.	Meliaceae	Sl	Wi	0.04	Ro	10.7	40.0	Or	Ep	Ph	Ph	No	12.66	AM, CA, CE, AF, PA, PT	FS, UAF, SDF, SEF, SSF, DRF
Terminalia corrugata (Ducke) Gere & Boatwr.	Combretaceae	Sl	Se	0.37	Fl	16.4	17.5	Or	Ep	Ph	Ph	Yes	11.64	AM, CA, CE	FS, DRF
Plathymenia reticulata Benth.	Fabaceae	Sl	Wi	0.10	Ov	9.1	17.5	Or	Ep	Ph	St	No	11.43	AM, CA, CE, AF	FS, GF, SSF, DRF
Anadenanthera colubrina (Vell.) Brenan	Fabaceae	Sl	Se	0.11	Ro	8.2	16.5	Or	Hy	Ph	St	No	11.28	CA, CE, AF	FS, SSF, DRF
Parapiptadenia rigida (Benth.) Brenan	Fabaceae	Sl	Se	0.03	Ro	9.9	21.5	Re	Ep	Ph	Ph	No	11.20	AF, PA	SDF, SSF, DRF
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	Malvaceae	Sl	Wi	0.15	Fl	5.7	25.0	Or	Hy	Ph	St	No	11.19	CE	FS
Senna multijuga (Rich.) S. S. Irwin & Barneby	Fabaceae	Fa	Wi	0.02	Fl	–	25.0	Or	Ep	Ph	Ph	Yes	10.55	AM, CA, CE, AF	FS, GF, UAF, SSF, DRF
Bowdichia virgilioides Kunth	Fabaceae	Sl	Wi	0.03	Fl	7.5	17.5	Or	Ep	Ph	Ph	Yes	10.54	AM, CA, CE, AF, PT	FS, GF, SEF, SSF
Astronium fraxinifolium Schott	Anacardiaceae	Sl	Wi	0.03	Ro	10.7	24.0	Or	Ep	Ph	Ph	No	10.18	AM, CE, AF	FS, SSF, GF
Dalbergia miscolobium Benth.	Fabaceae	Sl	Wi	0.05	Ro	7.1	17.5	Re	Ep	Ph	St	No	10.10	CE	FS, GF, SDF, SSF
Solanum lycocarpum A. St.-Hil.	Solanaceae	Fa	An	0.01	Ro	8.3	14.0	Or	Ep	Ph	Ph	No	9.28	CE, AF	FS, GF, SDF, SSF, DRF
Piptadenia gonoacantha (Mart.) J. F. Macbr.	Fabaceae	Fa	Se	0.05	Ro	–	19.0	Or	Ep	Ph	Ph	No	9.14	CE, AF	FS, GF, SSF, DRF, SDF
Enterolobium schomburgkii (Benth.) Benth.	Fabaceae	Sl	Se	0.28	Ov	–	16.0	Or	Ep	Ph	St	Yes	8.97	AM, CE	FS, GF, UAM
Astronium urundeuva (M. Allemão) Engl.	Anacardiaceae	Sl	Wi	0.02	Fl	12.0	22.5	Or	Ep	Ph	Ph	Yes	8.63	CA, CE, AF, PA, PT	FS, SDF, SSF,
Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	Fabaceae	Fa	An	0.03	Ov	–	15.5	Or	Ep	Ph	Ph	Yes	8.19	CA, CE, AF	FS, GF, SDF, SSF, DRF, AF
Schizolobium parahyba (Vell.) Blake	Fabaceae	Fa	Se	2.00	Fl	–	20.0	Or	Ep	Ph	Ph	Yes	8.03	AM, AF	SSF, DRF GF, UAF
Stryphnodendron adstringens (Mart.) Coville	Fabaceae	Sl	Se	0.11	Ov	7.4	17.5	Or	Ep	Ph	St	Yes	7.75	CA, CE	FS
Tachigali vulgaris L. G. Silva & H. C. Lima	Fabaceae	Sl	Wi	0.07	–	–	–	Or	Ep	Ph	Ph	Yes	7.52	AM, CA, CE	FS, SDF, SSF
Platypodium elegans Benth.	Fabaceae	Sl	Wi	1.08	Ro	11.1	37.5	Or	Hy	Cr	St	No	6.70	AM, CA, CE, AF	FS, GF, UAF, SDF, SSF, DRF
Bauhinia forficata Link	Fabaceae	Fa	Se	0.19	Ov	–	20.0	Or	Ep	Ph	Ph	No	6.11	AF, PA	GF, SSF, DRF, AF

Appendix 1. (continued)

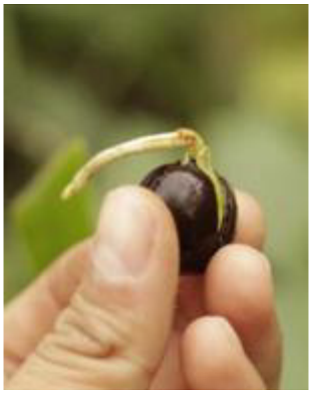
Species	Family	Functional traits[e]											E%[f]	Biome[g]	Forest type[g]
		GR	DS	SM[a]	SH[b]	SW[c]	GS[d]	ST	PC		EC	FC	SD		
Senegalia polyphylla (DC.) Britton & Rose	Fabaceae	Fa	Se	0.11	Ov	9.1	11.0	Or	Ep	Ph	St	No	5.75	AM, CA, CE, AF, PT	FS, GF, UAF, SSF, DRF
Croton floribundus Spreng.	Euphorbiaceae	Fa	Se	0.04	Ro	–	47.0	Or	Ep	Ph	Ph	No	5.54	AF	GF, SSF, DRF
Caryocar brasiliense Cambess.	Caryocaraceae	Sl	An	6.90	Fl	7.1	40.0	Re	Hy	Cr	St	Yes	5.10	AM, CA, CE, AF	FS
Ormosia arborea (Vell.) Harms	Fabaceae	Sl	An	1.33	Fl	–	55.5	Or	Hy	Ph	St	Yes	4.93	CE, AF	SSF, DRF
Amburana cearensis (Allemão) A. C. Sm.	Fabaceae	Sl	Wi	0.60	Ov	6.8	16.5	Or	Hy	Cr	St	Yes	4.86	CA, CE, AF, PT	FS, SDF, SSF
Myroxylon peruiferum L. f.	Fabaceae	Sl	Wi	0.44	Ov	–	12.5	Or	Hy	Cr	St	No	4.71	CE, AF	GF, SDF, SSF, DRF, AF
Solanum granulosoleprosum Dunal	Solanaceae	Fa	An	0.01	–	–	–	Or	Ep	Ph	Ph	Yes	4.70	CE, AF PA	FS, GF, SDF, SSF, DRF, AF
Schinus terebinthifolia Raddi	Anacardiaceae	Fa	An	0.01	Fl	12.6	40.0	Or	Ep	Ph	Ph	No	4.33	CA, CE, AF, PA	FS, GF, SSF, DRF, AF
Eremanthus glomerulatus Less.	Asteraceae	Fa	Wi	0.01	–	–	–	Or	–	–	–	Yes	4.12	CE	FS
Allophyllus edulis (A. St.-Hil. et al.) Hieron. ex Niederl.	Sapindaceae	Fa	An	0.03	Fl	–	26.5	Re	Ep	Ph	Ph	No	4.03	AM, CA, CE, AF, PA, PT	FS, GF, UAF, SSF, SDF, DRF, AF
Dimorphandra mollis Benth.	Fabaceae	Sl	An	0.17	Ov	4.6	22.5	Or	Ep	Ph	Ph	Yes	4.03	AM, CE, PT	FS, GF, SSF
Pterogyne nitens Tul.	Fabaceae	Sl	Wi	0.09	Ro	–	38.0	Or	Ep	Ph	Ph	Yes	3.68	CA, CE, AF	SDF, SSF
Terminalia argentea Mart.	Combretaceae	Fa	Wi	0.36	Ro	9.1	37.5	Or	Hy	Ph	St	No	3.41	AM, CA, CE, AF	FS, GF, SSF
Hancornia speciosa Gomes	Apocynaceae	Sl	An	0.14	Fl	18.5	26.5	Re	Ep	Ph	Ph	No	2.74	AM, CA, CE, AF	FS UAF, SDF, S
Guazuma ulmifolia Lam.	Malvaceae	Fa	An	0.01	Fl	8.8	30.0	Or	Ep	Ph	Ph	Yes	2.72	AM, CA, CE, AF, PA, PT	FS, UAF, SDF, SSF, DRF, AF
Trema micrantha (L.) Blume	Cannabaceae	Fa	An	<0.01	Fl	–	96.00	Or	Ep	Ph	Ph	Yes	2.25	AM, CA, CE, AF, PA, PT	GF, SSF, DRF
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae	Sl	Wi	0.04	Ro	11.5	35.0	Or	Ep	Ph	St	No	2.10	AM, CA, CE, AF, PA, PT	GF, UAFt, SSF, DRF, AF
Schinopsis brasiliensis Engl.	Anacardiaceae	Sl	Wi	0.15	Ov	10.3	38.0	Re	Ep	Ph	Ph	No	1.98	CA, CE	FS
Mimosa bimucronata (DC.) Kuntze	Fabaceae	Fa	Se	0.01	Ov	–	32.0	Or	Ep	Ph	Ph	Yes	1.87	CA, CE, AF, PA, PT	FS, SSF, DRF
Curatella americana L.	Dilleniaceae	Fa	An	0.02	Fl	13.6	31.0	Or	–	–	–	Yes	1.40	AM, CA, CE, AF	FS, GF
Croton urucurana Baill.	Euphorbiaceae	Fa	Se	0.01	Ro	–	30.0	Or	Ep	Ph	Ph	No	0.81	AM, CE, AF	GF, SSF, DRF
Colubrina glandulosa Perkins	Rhamnaceae	Fa	Se	0.02	Fl	15.9	37.0	Or	Ep	Ph	Ph	Yes	0.67	AM, CE, AF	FS, GF, UAF, SSF, DRF
Genipa americana L.	Rubiaceae	Sl	An	0.08	Ov	42.4	51.5	Or	Ep	Ph	Ph	No	0.26	AM, CA, CE, AF, PT	FS, GF, UAF, SDF, SSF, SEF, DRF

Appendix 1. (continued)

Species	Family	Functional traits[e]											E%[f]	Biome[g]	Forest type[g]
		GR	DS	SM[a]	SH[b]	SW[c]	GS[d]	ST	PC	EC	FC	SD			
Cordia trichotoma (Vell.) Arráb. ex. Steud.	Boraginaceae	Sl	Wi	0.05	Fl	51.7	72.0	Re	Ep	Ph	Ph	No	0.23	CA, CE, AF, PA	FS, SDF, SSF, DRF
Lafoensia pacari A. St.-Hil.	Lythraceae	Sl	Wi	0.03	Ro	17.5	34.5	Or	Ep	Ph	Ph	No	0.22	CE	FS, GF
Citharexylum myrianthum Cham.	Verbenaceae	Fa	An	0.06	Ov	14.2	45.0	Or	Ep	Ph	Ph	No	0.18	CA, CE, AF, PA	GF, SSF, DRF, AF
Heliocarpus popayanensis Kunth	Malvaceae	Fa	Wi	<0.01	Ro	–	35.0	Re	Ep	Ph	Ph	Yes	0.17	AM, CE, AF	DRF
Annona crassiflora Mart.	Annonaceae	Sl	An	0.50	Fl	7.1	–	Or	Hy	Cr	St	No	0.07	AM, CE, PT	FS
Cecropia pachystachya Trécul	Urticaceae	Fa	An	<0.01	Fl	–	32.5	Or	Ep	Ph	Ph	No	0.00	AM, CA, CE, AF, PA, PT	FS, GF, SSF, DRF, AF
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Bignoniaceae	Sl	Wi	0.02	Ro	–	39.0	Or	Ep	Ph	St	No	0.00	CE, AF, PA	FS, DRF
Luehea divaricata Mart. & Zucc.	Malvaceae	Fa	Wi	0.06	Ov	15.6	20.5	Or	Ep	Ph	Ph	No	0.00	CA, CE, AF, PA, PT	FS, GF, SDF, SSF
Tachigali aurea Tull	Fabaceae	Sl	Wi	0.09	–	–	28.0	Or	Ep	Ph	Ph	Yes	0.00	CE	FS, GF
Zanthoxylum rhoifolium Lam.	Rutaceae	Sl	An	0.02	Fl	11.2	80.0	Or	Ep	Ph	Ph	Yes	0.00	AM, CA, CE, AF, PA, PT	FS, GF, UAF, SSF, SDF, DRF

[a] Mass of one seed (g). [b] Variance of three seed dimensions (length, width, and thickness) after each value was divided by the largest: flat ≤ 0.09, oval = 0.09 to 0.20, and round ≥ 0.20. [c] Amount of water in the seed (%). [d] Median of minimum and maximum germination days (days). [e] Functional traits were obtained from the literature (Carvalho 2003, 2006, 2008; Ressel et al. 2004; Mori et al. 2012; Frigieri et al. 2016; Souza-Júnior and Brancalion 2016; Zambrano 2017; Consolaro et al. 2019; Ribeiro et al. 2022). **Functional traits:** *Growth rate* (GR): Fa (fast) or Sl (slow); *Seed dispersal syndrome* (DS): An (animal-dispersed), Se (self-dispersed), or Wi (wind-dispersed); *Seed mass* (SM), g; *Seed shape* (SH): Fl (flat), Ov (oval), or Ro (round); *Seed water content* (SW), %; *Germination speed* (GS), days; *Seed storage class* (ST): Or (orthodox) or Re (recalcitrant); *Position of cotyledons* (PC): Ep (epigeal) or Hy (hypogeal); *Exposition of cotyledons* (EC): Ph (phanerocotylar, expanded and exposed during germination) or Cr (cryptocotylar, not expanded during germination); *Function of cotyledons* (FC): Ph (photosynthetic) or St (storage); *Seed dormancy* (SD): Yes or No; **E%:** percent establishment; **Biome:** (AM) Amazon, (CA) Caatinga, (CE) Cerrado, (AF) Atlantic Forest, (PA) Pampa, or (PT) Pantanal; **Forest type:** (FS) Forested Savanna, (GF) Gallery Forest, (UAF) Upland Amazon Forest, (SSF) Seasonal Semideciduous Forest, (DRF) Dense Rainforest, (SDF) Seasonal Deciduous Forest, (AF) Araucaria Forest, or (SEF) Seasonal Evergreen Forest. [f] Percentage of established seedlings in the field, in relation to the number of seed sown. [g] JBRJ (2024), available at https://floradobrasil.jbrj.gov.br (last accessed 27 Jan. 2025).

Notes: Tree nomenclature follows that of Reflora Project, Rio de Janeiro Botanical Garden (https://floradobrasil.jbrj.gov.br, last accessed 27 Jan. 2025). Additional species not listed by Souza (2023) but reported by Caminhos da Semente (https://www.caminhosdasemente.org.br/especies) as having between 20% and 60% field establishment rate include taxa from several Families: Anacardiaceae: *Anacardium occidentale* L.; Bignoniaceae: *Handroanthus ochraceus* (Cham.) Mattos; Bixaceae: *Bixa orellana* L.; Boraginaceae: *Cordia alliodora* (Ruiz & Pav.) Cham.; Fabaceae: *Dipteryx odorata* (Aubl.) Willd., *Hymenaea martiana* Hayne, *Machaerium pedicellatum* Vogel, *Piptadenia macradenia* Benth, *Schizolobium parahyba var. amazonicum* (Huber ex Ducke) Barneby, *Tachigali subvelutina* (Benth.) Oliveira Filho; Loganiaceae: *Strychnos pseudoquina* A. St.-Hil.; Malpighiaceae: *Byrsonima coccolobifolia* Kunth; Malvaceae: *Eriotheca gracilipes* (K.Schum.) A.Robyns, *Pseudobombax grandiflorum* (Cav.) A. Robyns, *Sterculia striata* A. St.-Hil. & Naud., *Sterculia apetala* (Jacq.) H. Karst.



Seeding acorns for montane cloud forest restoration in central Veracruz, Mexico: practical experiences

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Abstract

Tropical montane cloud forests in Mexico, though rich in unique species, cover less than 1% of the country and face severe deforestation and ongoing threats, especially to oaks (*Quercus* spp.). Our study in the montane cloud forests in the Jamapa and La Antigua River basins of central Veracruz tested acorn seeding for forest restoration. Field trials were conducted across peri-urban and rural secondary forests, employing a range of acorn protection devices (e.g., wire mesh cages, chili pepper (*Capsicum* spp.) covering) and site preparation techniques to mitigate predation by rodents (Order Rodentia) and other fauna. The study also assessed the influence of microsite selection and pre-germination treatments on seedling emergence. Various rodents were the main obstacle to seeding success, exclusion devices like wire mesh cages greatly improved outcomes. Effectiveness depended on species, site, and year. Chili pepper coverings did not deter birds, and they exposed the acorns to seed predators. Successful restoration requires careful microsite selection; acorns are less preyed upon by rodents in areas with low to moderate vegetative cover. Seeds should be collected from multiple mother trees during peak fall and inspected for viability. When storage is needed, acorns should be stored under controlled conditions to maintain moisture and prevent fungal contamination. Acorn masting leads to variable seed availability modulating seed predation patterns; mast years are optimal for seeding projects. These findings underscore the need for adaptive, site-specific restoration protocols, including rapid pilot trials and monitoring of acorn production cycles.

Keywords

Quercus, acorn seeding, seed predation, mast years, rodent exclusion devices

Contents

1 The forest

1.1 Physiographic region

Our study area is in the mountainous regions of the Jamapa and La Antigua River basins in central Veracruz, Mexico (Figure 1a, area ≈ 1600 km^2). These river basins are considered priorities for urgent conservation and restoration actions, and the region is a biodiversity hotspot due to the convergence of the Nearctic and Neotropical regions (Cotler et al. 2010; Gómez-Díaz et al. 2023; Toledo-Aceves et al. 2011). Land use in the region is comprised of agricultural crops, shade coffee (*Coffea arabica* L.) plantations, cattle (*Bos taurus*) pastures, secondary cloud forests, and remnants of conserved tropical montane cloud forest (TMCF) (CONABIO 2010). The TMCF fragments in this area are distributed mainly along an elevational gradient from 1000 to 2400 masl. At the lower and upper extremes of this gradient, the mean annual temperatures are 18 and 12 °C, and annual precipitation is 1700 and 1200 mm, respectively, with the highest precipitation (2200 mm) occurring at the middle of the gradient (Williams-Linera et al. 2013). Soils are mainly Andosols with abundant organic matter and Luvisols at the lower elevations in the landscape (Williams-Linera 2012; Williams-Linera et al. 2013). Three well-defined seasons occur in the region: a cold dry season from late October–November to March, a hot dry season from April to May, and a hot wet season from June to September–October (Williams-Linera 2012; Williams-Linera et al. 2013). Global climate models suggest higher temperatures at higher elevations in the next century, and uncertainty remains regarding the effects of temperature and moisture changes on cloud formation in mountainous regions because the cloud base could lift in response to higher temperatures (Foster 2001; Salinas et al. 2021).

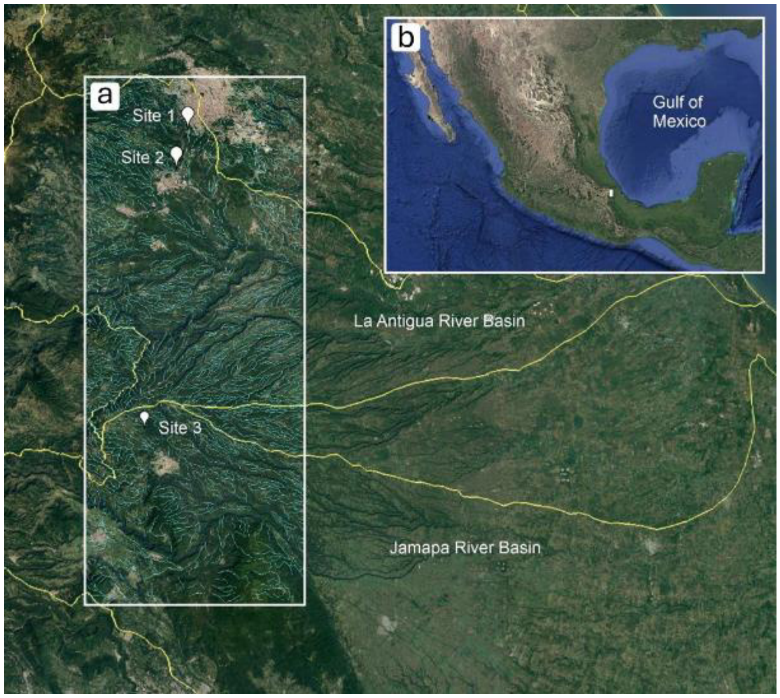

Figure 1. (a) Location of the mountainous regions in the Jamapa and La Antigua River basins in central Veracruz, Mexico (rivers are delineated as ephemeral (light blue) and permanent (dark blue). (b) Location of the study area relative to Veracruz State and the Gulf of Mexico. (Photo credits: (a–b) Google Earth, Images from 2024).

1.2 Forest type

The TMCF has a fragmentary distribution and occupies only 0.5 to 1% of Mexican territory. This forest type is present in mountainous areas with steep topography, particularly in areas protected from solar radiation and strong winds. It is characterized by the frequent presence of clouds and fog (Rzedowski 1996). In Mexico, TMCF is the forest type with the highest floristic richness per unit area, the estimated habitat of more than 3000 species of vascular plants (about 10–12% of plant richness in the country), of which about 30% are endemic (Rzedowski 1996; Williams-Linera 2012). In central Veracruz, Williams-Linera et al. (2013) recorded two groups of forests defined by elevation and tree species composition: lower (1250 to 1630 masl) and upper (1800 to 2550 masl) montane forest. The canopy and overstory of lower montane forests are dominated by *Quercus lancifolia* Schltdl. & Cham., *Q. sartorii* Liebm., *Q. xalapensis* Bonpl., *Carpinus tropicalis* (Donn.Sm.) Lundell, *Clethra macrophylla* M. Martens & Galeotti, *Liquidambar styraciflua* L., and *Turpinia insignis* (Kunth) Tul., whereas the canopy of the upper montane forest is dominated by *Q. corrugata* Hook., *Prunus rhamnoides* Koehne, *Cleyera theaeoides* (Sw.) Choisy, *Ternstroemia sylvatica* Schltdl. & Cham., and *Weinmannia pinnata* L. TMCF fragments are highly diverse and heterogeneous in structure. Trujillo-Miranda et al. (2018) evaluated a mature forest fragment and 21-year-old secondary forests, documenting average tree heights of 25 and 14 m, mature tree densities of 614 and 350 trees ha^{-1}, and basal areas of 44 and 12 m^2 ha^{-1}, respectively. Commercially valuable tree species include *Juglans pyriformis* Liebm., *Oreomunnea mexicana* (Standl.) J.-F.Leroy, *Quercus spp., Trema micrantha* (L.) Blume, and *L. styraciflua* (Toledo-Aceves et al. 2021a).

1.3 Deforestation and degradation of the forest

In central Veracruz, TMCF has been deforested and converted mainly into coffee, sugarcane (*Saccharum officinarum* L.) plantations, and pastures, while the main recent threat is the conversion of remnant forest patches to urban and suburban housing (Toledo-Aceves et al. 2011). In this region, an annual TMCF cover change of −0.44% was estimated for the period from 1993 to 2000, although a low positive rate of forest cover gain (0.11%) was recorded in 2000–2014 (Gómez-Díaz et al. 2018). In addition to forest conversion, there are other causes of degradation, including selective illegal logging and hunting, environmental contamination, and climate change. Climate change is projected to cause the loss of populations of threatened and endangered cloud forest trees (Jiménez-García and Peterson 2019). The genus projected to undergo the most serious negative effects is *Quercus*, which is also the most important genus in this biome. Land use change could exacerbate the negative impacts of climate change (Gómez-Díaz et al. 2018; Rojas-Soto et al. 2012).

2 Impacts of deforestation and degradation on candidate restoration sites

2.1 Site degradation

Three sites illustrate the degradation history and high heterogeneity in their areas. Site 1 is a 30-ha peri-urban forest (old-secondary forest; 1250 masl) bordering the city of Xalapa and comprised of a vegetation mosaic that includes preserved TMCF patches and regenerating secondary and degraded forests (Williams-Linera et al. 2013). In the 1940s, some patches were plantations of coffee or citrus (*Citrus* spp. L.), and featured a canopy formed by exotic species planted to provide shade, together with native species. These plantations were abandoned in the 1980s, but patches with some exotic fruit species (such as *Citrus* spp. and loquat, *Eriobotrya japonica* (Thunb.) Lindl.) can still be found.

Site 2 is a 2.5 ha young secondary forest located northeast of Coatepec, Veracruz (5 km from Site 1), at an elevation of 1200 masl. Cattle were excluded from this site from 2019 onward, and the mosaic of secondary vegetation consists of areas dominated by exotic grasses such as *Cynodon dactilon* (L.) Pers. and *Paspalum spp*. L. and woody pioneer species including *Vernonia patens* Kunth. *Heliocarpus appendiculatus* Turcz., *H. donnellsmithii* Rose, and *Cnidoscolus multilobus* (Pax) I.M.Johnst. among others. Active restoration has been implemented at this site since 2020.

Site 3 is a mosaic of passively and actively restored secondary forest fragments (around 61 and 37 ha, respectively) located in the municipality of Huatusco (1500 masl). This TMCF site was deforested and transformed into cattle pastures in 1950; exotic grasses were introduced (e.g., *Cynodon plectostachyus* (K.Schum.) Pilg., *Brachiaria decumbens* Stapf, *Setaria sphacelata* (Schumach.) Stapf & CE Hubb. ex Moss, and *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs). Livestock were excluded from the grazing areas in 1995, and passive and active restoration interventions have since taken place.

2.2 Damaging agents

Despite the different disturbance regimes of the restoration sites, common factors limit tree regeneration (seed and seedling survival and sapling establishment). At study Site 3, there is low regeneration of late-successional trees dispersed by gravity and animals (barochory and zoochory) compared to regeneration in the adjacent mature forest fragment (Toledo-Aceves et al. 2021b). Bird and mammal seed dispersers in the landscape are affected by habitat loss, forest isolation, edge effects, urban roads, illegal hunting, and feral fauna. In the defaunated secondary forest fragments, some small rodents (Order Rodentia), such as squirrels (Family Sciuridae), sustain their populations mainly through seed predation, especially acorns.

Seedling emergence and establishment are limited by abiotic microhabitat constraints, competition from patches of exotic grasses, vines, shrubs (e.g. *Rubus* spp. L., *Piper* spp. L.), and especially the fern *Pteridium arachnoideum* (Kaulf.) Maxon (Toledo-Aceves et al. 2022). Herbivory of seedlings by gophers (*Heterogeomys hispidus* Le Conte) and rabbits (*Sylvilagus floridanus* J.A. Allen) is another important but less evaluated limiting factor at all the restoration sites (Ortega-Pieck et al. 2011). At some sites, cattle foraging also impacts seedling survival, particularly along forest edges. Seedlings and saplings are exposed to physical and physiological damage due to extreme weather events such as wind and rainstorms, heat waves, and flooding and landslides.

3 Mitigating impacts for acorn seeding

3.1 Damage

Oaks are key tree species for forest restoration in the region because they are forest foundational species and exhibit relatively high survival and growth on degraded sites. However, acorn predation is widely documented as the most important filter for the feasibility of seeding as a restoration strategy (Löf et al. 2019). Acorns are consumed by insects, birds, and mammals (Bartlow et al. 2018). In the study areas, squirrels and mice (Family Muridae) are the main active removers of acorns. Some buried, superficial, or mixed devices have been developed to prevent acorn removal and *in situ* predation (Figure 2a–d). Castro et al. (2015) developed an effective plastic device that is half buried, with two small openings at the top and bottom where the stem and root can emerge, and limits rodent access to the acorn held in the interior (Figure 2a). Wire mesh devices have also been developed, with relative success at preventing acorn removal by small mammals. Some of these devices are designed to prevent underground acorn removal (Figure 2b; Reque and Martin 2015). At Site 1, wire mesh cages fixed to the ground were used to protect acorns of four oak species, and this technique was found to be highly effective because it prevented access by vertebrates for 184 days, allowing 22.5% of the seeded acorns to establish a seedling (Figure 2c; García-Hernández and López-Barrera 2024). Although wire cages are easily produced and reusable, these types of devices must be removed before they interfere with seedling development (Figure 2c), thereby increasing their cost, especially when utilized on a large scale (Löf et al. 2019).

The best acorn protection technique should effectively reduce predation with no effect on germination (radicle extension), seedling emergence (plumule extension), or plant development, maintain the cost advantage of seeding over planting seedlings, and be environmentally sustainable. One method to deter seed predators is coating acorns with capsaicin, a compound found in chili peppers (*Capsicum* spp. L.) that irritates some animals. However, this method can affect seedling emergence because high capsaicin concentrations can affect plumule emergence (Leverkus et al. 2013). At Site 2, Brewster-Salmones et al. (2024) evaluated the protection provided by chili peppers (*C. annuum* L. and *C. pubescens* Ruiz & Pav.) to acorns of *Q. germana* Schltdl. & Cham., an endangered endemic oak tree of the cloud forest. This technique did not affect germination or seedling emergence (Figure 2d); however, the peppers did not result in protecting acorns because birds consumed the chili peppers.

Germination rate could influence acorn fate, depending on seed predator type and population size. Buried and pre-germinated acorns confer the advantage of reducing predation and accelerating the transition from seed to seedling (Figure 2d). However, when seed predator populations are abundant, even buried and germinated acorns can be found and consumed. For instance, acorns of white oak (Section Quercus) species germinate immediately upon seed fall, but squirrels detect them by their odor, removing the embryos before the seeds are cached. In the case of red oak (Section Lobatae) acorns that show dormancy, squirrels prefer to cache intact acorns for subsequent consumption (Steele et al. 2001). At Site 1, *Q. pinnativenulosa* C.H. Mull. acorns were buried 1 to 2 cm below the forest litter (Rodríguez-Zambrano 2024). Pre-germinated acorns had lower predation than non-germinated seeds (Table 1). The high level of acorn predation can be attributed to the high populations of squirrels and mice and the constant acorn production in this peri-urban secondary forest fragment. However, at Site 2, a pilot study by Vivar-Vázquez (unpublished data) showed that burying pre-germinated acorns of *Q. xalapensis* successfully avoided acorn removal during a cold winter (Figure 2d, Figure 4e, Table 1). Rodent activity can be modulated by climatic variability with cold winters reducing rodent metabolism and activity. At this site, however, rodent populations seemed to be highly variable and there were no mast-producing oaks in the canopy.

Table 1. Field evaluations of germination and emergence of oak (*Quercus* spp.) species of tropical montane cloud forests in Mexico.

Species	Year	Acorn removal/predation (%)				Acorn germination (%)			Seedling emergence (%)			
		A	B	C	D	A	B	D	A	B	C	D
Q. germana Schltdl. & Cham.[a,b]	M	56	22–0	–	–	20	58–78	–	4	8–20	–	–
	NM	68.3	–	–	77.5–80.8	30.8	–	36.6–42.9	–	–	–	–
Q. insignis M.Martens & Galeotti[c]	M	97.0	–	–	–	25.3	–	–	1.0	–	–	–
	NM	88.3	–	–	–	1.7	–	–	0.0	–	–	–
Q. lancifolia Schltdl. & Cham.[a]	M	74	46–0	–	–	14.0	28–54	–	4.0	16–32	–	–
Q. *pinnativenulosa* C.H.Mull.[d]	M	44.7	–	25.8	–	–	–	–	2	–	14.7	–
Q. sartorii Liebm.[a]	M	50	34–0	–	–	0.0	4–22	–	0.0	2–4	–	–
Q. xalapensis Bonpl.[a]	M	72	58–0	–	–	14.0	12–62	–	6.0	4–34	–	–

[a] García-Hernández and López-Barrera 2024. [b] Brewster-Salmones et al. 2024. [c] García-Hernández et al. 2025. [d] Rodríguez-Zambrano 2024. M = mast year. NM = Non-mast year. Treatments: A = Seed not pre-germinated and sown without protection. B = Partial - total exclusion. C = Pre-germinated acorns. D = Chili pepper protection.

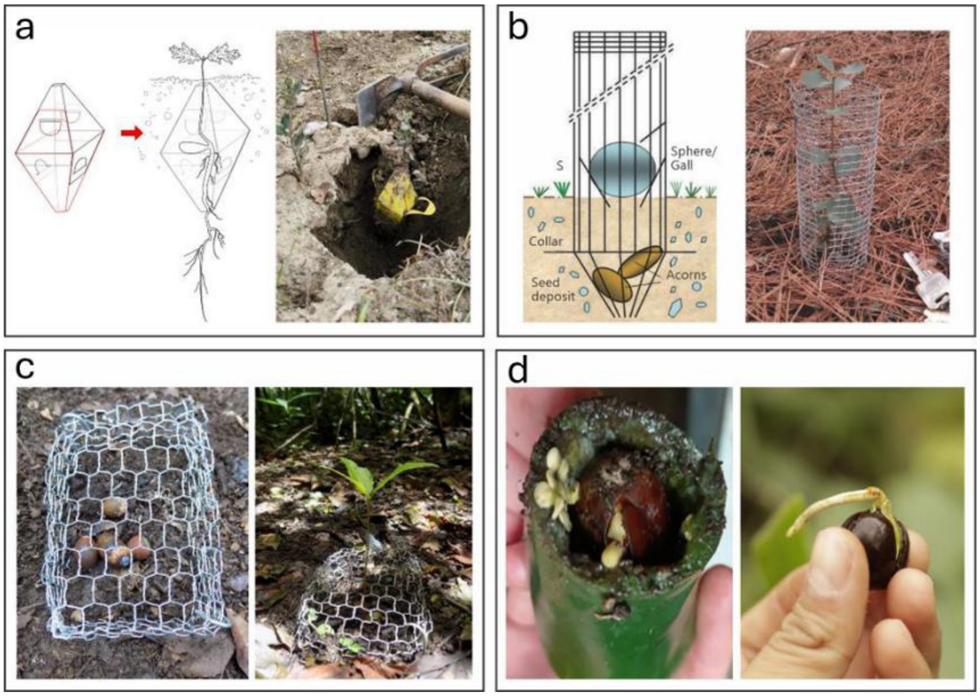

Figure 2. Devices and strategies used to reduce acorn predation. (a) Seed shelter (total protector). (b) Seed total protector. (c) Wire cages implemented at Site 1 (total protections). (d) Examples of partial protection, *Q. germana* Schltdl. & Cham. acorns inserted in *Capsicum annum* L. fruit implemented at Site 2) and pre-germinated acorns of *Q. xalapensis* Bonpl. to reduce acorn predation at Site 2 (Photo credits: (a) Castro et al. (2015), (b) Reque and Martin (2015), (c) García-Hernández and López-Barrera (2024), (d) Brewster et al. (2024) and Dulce C. Vivar-Vázquez).

3.2 Site preparation

In degraded areas, seeding microsite types should be considered as they influence presence and foraging patterns of rodents. Acorns are at greater risk of predation by rodents that prefer to forage in microsites with high vegetative cover from various strata, such as herbaceous plants, shrubs, small and large trees, under and near shelterwoods, and woody debris and slash piles. Thus, it is advisable to bury acorns at sites with low to moderate vegetative cover and avoid log piles that can provide shelter for rodents (García-Hernández et al. 2016; García-Hernández and López-Barrera 2024). Nevertheless, vegetative cover helps maintain acorn moisture, acting to promote germination and emergence.

Striking a balance is necessary between the microenvironmental requirements for seedling establishment and the risk of acorn predation. The different foraging patterns of the faunal assemblage should also be considered, even when using acorn protection to deter rodent predation. For example, Leverkus et al. (2015) reported that a protective device was effective in preventing rodent predation in the Mediterranean region, but its effectiveness against wild boar (*Sus scrofa*) predation was dictated by microhabitat complexity.

4 Seed procurement and preparation

4.1 Collection

Masting, the episodic production of seed crops in some years, followed by one or more years of low or no mast (Steele 2021), has been reported for some oak species. In central Veracruz, the studied oak species alternate their production with heavy mast in one year followed by another year with low or very low acorn production. This has also been reported for two oak species in the highlands of Chiapas, Mexico, where acorn production can be 8 to 9 times greater in a mast year than in the following non-mast year (161 ± 19 vs. 21 ± 3 acorns m^{-2}, respectively; López-Barrera et al. 2007). The oak having the largest seed at Site 3, *Quercus insignis* M. Martens & Galeotti presented an even higher difference of 25 times greater acorn production in the mast year than in non-mast year (García-Hernández et al. 2025).

Low production and high predation rates could delay or impede the implementation of an enrichment restoration project in degraded or secondary forests. It is also crucial to consider the variation in seed production for each species for the purposes of project planning and implementation because this affects acorn quantity and quality. Acorn availability in relation to the seeding field trials from our study sites is shown in Table 1. For secondary forests in a non-mast year (Sites 1 and 3), a large part of the crop was predated while still on the tree; the acorns that survived to mature and fall to the forest floor were quickly removed by fauna (García-Hernández et al. 2025; López-Barrera et al. 2007).

Although it is advisable to collect seed from many individuals to guarantee high genetic variability (Vander Mijnsbrugge et al. 2010), in the case of species that have restricted distribution or drastically reduced populations, it is not always possible to include a large number of mother trees. For our study sites, the number of mother trees sampled for acorn collections ranged from three to 10 individuals per species. A particular oak species can exhibit a different fruiting period depending on the region in which it is found, and it is therefore important that planning includes the monitoring of potential mother trees to determine the appropriate time for acorn collection.

Collecting acorns during peak fall increases the probability of suitable seed quality and viability. A mature acorn is partially or completely brown (Figure 3h–i) and heavier than the immature, damaged, or non-viable seeds when it falls from the tree (Rodríguez-Acosta and Coombes 2020). In central Veracruz, acorn fall occurs mainly in autumn, from mid-October to mid-December. Acorns used in this research were collected in late October and early November. However, in recent years, some species have released their seed in early September or delayed their release until mid-winter.

Acorns are typically collected directly from the ground, although this can be done using seed traps or, where possible, directly from the tree (Figure 3a–c). Although it has been reported for different species that large seeds produce individuals with greater growth and biomass acquisition (Baraloto et al. 2005; García-Hernández et al. 2023), size selection could inadvertently reduce genetic variability. Thus, given the low number of mother trees for some species, seeds of all sizes encountered were included in our studies, and only fully developed (mature) and healthy (no bite marks or weevil (*Curculio* spp. L.) larvae exit holes) seed were collected (Figure 3d–i). Acorns having evidence of partial predation are generally considered to have poor performance and are discarded. However, one study showed that acorns of *Q. insignis*, the largest-seeded oak species in the world, can lose up to 30% of its total size (Figure 3f) with no reduction in germination and emergence values (García-Hernández et al. 2023).

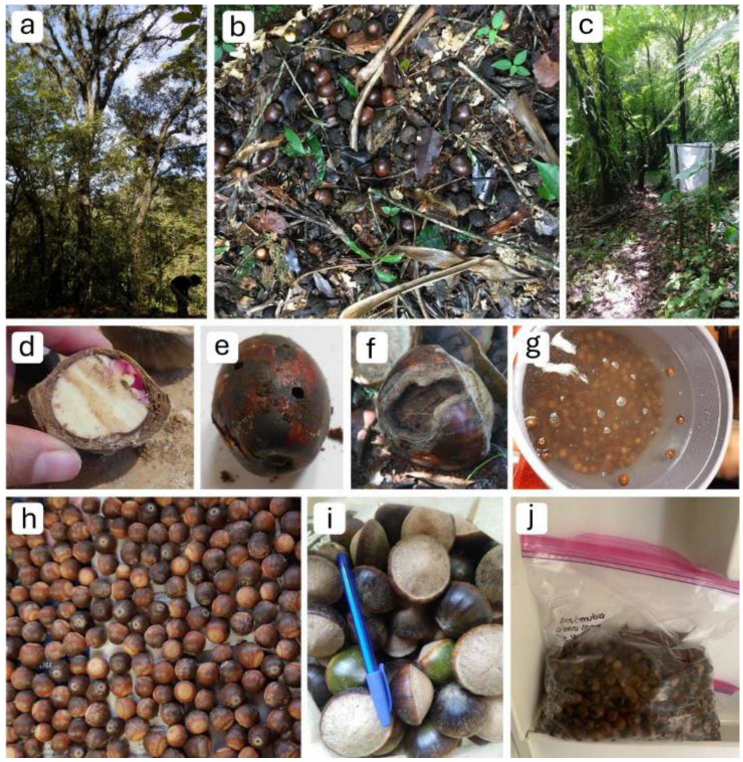

Figure 3. (a–b) Collecting acorns of *Q. lancifolia* Schltdl. & Cham. directly from the ground. (c) Seed trap placed in the forest (Site 3). (d) Transversal cut of a healthy *Q. insignis* M. Martens & Galeotti acorn. (e) Non-viable acorn with exit holes left by the emergence of weevil larvae. (f) Acorn partially damaged by rodents. (g) Float method to discard non-viable acorns. (h–i) Mature and healthy acorns of *Q. xalapensis* Bonpl. and *Q. insignis* M. Martens & Galeotti. (j) Acorns prepared for cold storage. (Photo credits: (a–e) Ma. de los Ángeles García-Hernández, (f) Fabiola López-Barrera, (g–h) Dulce C. Vivar-Vázquez, (i) Ma. de los Ángeles García-Hernández, (j) Dulce C. Vivar-Vázquez).

After collection, in addition to visual inspection to identify dried or damaged seed (Figure 3e and 3f), all seed were subjected to the buoyancy test to eliminate apparently non-viable seed (Gribko and Jones 1995). It is important to note that this technique is not 100% effective in detecting seed having weevil larvae that have yet to emerge (Figure 3g). For this reason, a second acorn inspection should also be conducted at the time of sowing. Seed of each studied species were stored in labeled (collection site, date, species, tree number) plastic (polyethylene) bags (Figure 3j) and transported to the Functional Ecology Laboratory of The Institute of Ecology A.C. (INECOL).

4.2 Handling

Where necessary, each acorn was separated from its cupule and dirty seed were cleaned, inspected again to discard damaged individuals, and buoyancy tested. Prior to storage, excess moisture was removed with a dry cloth to prevent fungal contamination. Studies indicate that acorn moisture content below 30 to 40% affects viability (Liu et al. 2024; Schroeder and Walker 1987). Acorns are recalcitrant and sensitive to desiccation, which will affect their viability, so care must be taken to avoid drying the seed too much when handling. Oak species mainly distributed in humid montane forests typically have desiccation sensitive acorns because rain and high humidity are present most of the year (Kang et al. 2023). However, exposure to excessive moisture for extended periods can reduce germination due to fungal decomposition.

4.3 Storage and stratification

All viable seeds of each species were stored in labeled plastic bags and refrigerated at 4 to 7 °C until sowing in the field (in our studies a maximum of three weeks). Seed (particularly white oaks) can germinate or mold when stored in a dark refrigerator if there is sufficient humidity, so they must be checked at least every third day. Maximum storage time will depend on species (oaks with rapid germination vs. oaks with dormancy), seed lot quality, humidity at the time of collection, and temperature (Liu et al. 2024; Rodríguez-Acosta and Coombes 2020; Schroeder and Walker 1987).

4.4 Preparing seeds for the field environment

Soaking acorns for a few hours prior to sowing could promote germination (Rodríguez-Acosta and Coombes 2020) and hydrated seed brought to the field might be more able to withstand climatic variability on degraded sites. Pre-germinated seed (radicle of 1 to 3 cm) can be transported to the field; this practice is particularly beneficial for red oak species that show dormancy. There are several techniques to pre-germinate acorns, such as using a germination chamber at a temperature of 26 to 28 °C (Rodríguez-Acosta and Coombes 2020; Vivar-Vázquez unpublished data). Sowing pre-germinated seed of *Q. pinnativenulosa* resulted in faster seedling emergence compared to untreated seed (Rodríguez-Zambrano 2024). At Sites 1 and 3, acorns that were not pre-germinated were used in our study and marked with a wax pencil to distinguish individuals in the field (Figure 2c). At Site 2, acorns inserted in chili peppers were used as part of a study to determine the protective effect of the peppers for predation prevention and facilitation of germination (Figure 2d; Brewster et al. 2024).

5 Plantation establishment

5.1 Plantation design

Oak species in sections Quercus (*Q. germana*, *Q. insignis*, and *Q. lancifolia*) and Lobatae (*Q. xalapensis* and *Q. sartorii*) have been used in seeding experiments (Table 1). Rodríguez-Zambrano (2024) also introduced *Q. pinnativenulosa* (Section Lobatae) at Site 1. Seeding practices with oaks are directed plantings in terms of sowing density and selected microsites (see above, Site Preparation). For example, in the case of Site 1, one acorn of each species (*Q. germana*, *Q. lancifolia*, *Q. xalapensis*, and *Q. sartorii*) was sown at each sowing spot (Figure 4d). In each selected microsite, sowing a single or few seeds (2 to 4) may increase their survival because predators have less chance of discovering small seed groups. In some cases, as in Site 3, 15 *Q. insignis* acorns were sown per microsite (Figure 4c) to benefit identification of seed predators captured with camera traps. Sowing density can therefore be modified according to objectives. Distance between microsites can vary according to site size and distribution of the best microsites for sowing. Examples from our work includes minimum distances between sowing microsites of 10 to 15 m (Brewster-Salmones et al. 2024), 15 to 20 m (García-Hernández and López-Barrera 2024), and up to 40 m at larger sites such as Site 3 (García-Hernández et al. 2025).

Figure 4. (a) Sowing acorns at Site 1. (b) Total protection using metal stakes to fix the wire cage to the ground. (c) Sowing unprotected *Q. insignis* M. Martens & Galeotti acorns at Site 3. (d) Comparing two wire-cage types (total protection) and unprotected acorns from four oak species at the same seeding microsite. (e) Emerged seedlings (*Q. xalapensis* Bonpl.) at Site 2 from partially protected (*Capsicum* spp. L. fruits) and unprotected acorns illustrating for this site and year (cold winter) that there was no need to protect acorns (Photo credits: (a–d) Ma. de los Ángeles García-Hernández, (e) Dulce C. Vivar-Vázquez).

5.2 Sowing practices

In our studies, seed were sown at selected microsites during the natural period of acorn fall and seedling recruitment (autumn). Monitoring was extended up to 184 days depending on the time required for germination and emergence of seedlings of each species (Table 2). Whether or not to bury acorns with soil, leaf litter, or plant debris from each site depends on several factors. If the seed are protected and the restoration site has tree cover with low microclimate variation at the forest floor, acorns can be sown on leaf litter, left unburied to avoid rotting. If acorn protection is not planned for use due to a low density of predators or deployment of pre-germinated seed, it is advisable to bury acorns 2 to 4 cm deep to avoid detection and predation. Likewise, if acorns are protected but the site is open, such as a recently abandoned pasture, they can be buried under plant litter to avoid desiccation. Because acorn removal and predation patterns were known for some species at Site 1 (García-Hernández et al.

2016), different rodent exclusion treatments were applied: total exclusion, partial exclusion (access by mice only), and no exclusion (Figure 4d). Cages made with mesh wire of various mesh sizes were used. The cages covered the seed but allowed water and light to enter. Each cage was fixed to the ground with metal stakes to prevent lifting by squirrels (Figure 4b). At Site 2, seeds were embedded in chili peppers (*C. pubescens* or *C. annum*), which were placed above ground and accessible to all predators (Figure 2d). At Site 2, Vivar-Vázquez (unpublished data) placed intact pre-germinated acorns under plant debris and grass litter, while all *Q. insignis* seed at Site 3 were exposed with no protection (Figure 4c). Given that this species has the largest acorns, varying from 10 to 86 g, its size may modulate acorn removal, predation and dispersal by small mammals (García-Hernández et al. 2025).

Table 2. Greenhouse evaluation of germination and emergence of oak (*Quercus* spp.) species of tropical montane cloud forests in Mexico.

Section	Species	Mean acorn mass ± SE	Acorn germination (%)	Seedling emergence (%)	1-2 weeks	2-4 weeks	1-2 months	2-4 months	4-6 months
Quercus	*Q. germana* Schltdl. & Cham.	14.5 ± 4.8[a]	80.0	31.4					
		10.6 ± 0.2[b]	66.0	–					
		11.7 ± 0.5[c]	85	67.5					
		18.1[d]	18.1	–					
	Q. insignis M.Martens & Galeotti	34.5 ± 0.4[b]	55.0	37.7					
		45.2 ± 0.70[e]	46.7	38.5					
	Q. lancifolia Schltdl. & Cham.	4.82±0.15[c]	83.3	78.3					
Lobatae	*Q. pinnativenulosa* C.H.Mull.	1.20±0.05[g]	42	29					
	Q. sartorii Liebm.	3.05±0.03[b]	70.3	53.7					
		2.24±0.05[c]	15.8	13.3					
	Q. xalapensis Bonpl.	2.77± 0.04[b]	60.0	60.0					
		3.2 ± 0.1[c]	48.0	46.7					
		3.1 ± 0.1[f]	47.5	37.5					

[a] Brewster-Salmones et al. 2024. [b] García-de la Cruz et al. 2016. [c] García-Hernández and López-Barrera 2024. [d] Toledo-Aceves et al. 2017. [e] García-Hernández et al. 2023. [f] Vivar-Vázquez (unpublished data). [g] Rodríguez-Zambrano 2024. = acorn germination, = seedling emergence, = seedling > 15 cm tall.

6 Post-sowing practices and maintenance

Most restoration ecology studies of acorn seeding are concluded after measurement of seedling emergence (Figure 5). In our case, monitoring for more than 100 days allowed us to determine the time required for each species to transition from germination to plumule emergence, to establishment of vigorous and competitive seedlings that exceeded 15 cm tall (Table 2). Many of the experiments at our three sites have evaluated the factors that limit early seedling establishment. Some practices that increased seedling survival included seeding in open areas but under partial shade from isolated trees (*Q. insignis*; Montes-Hernández and López-Barrera 2013) or performing 3 to 4 annual releases from exotic grass competition until the seedlings outgrew the weeds (Williams-Linera et al. 2015). No additional measures have been used to protect seedlings, although cattle have been excluded from the sites. Herbivory events have been observed sporadically but the resprouting capacity of some oaks allows them to persist. Additionally, it is still necessary to evaluate whether established seedlings may be favored in their growth by releasing them from the understory in different microhabitats within the degraded areas.

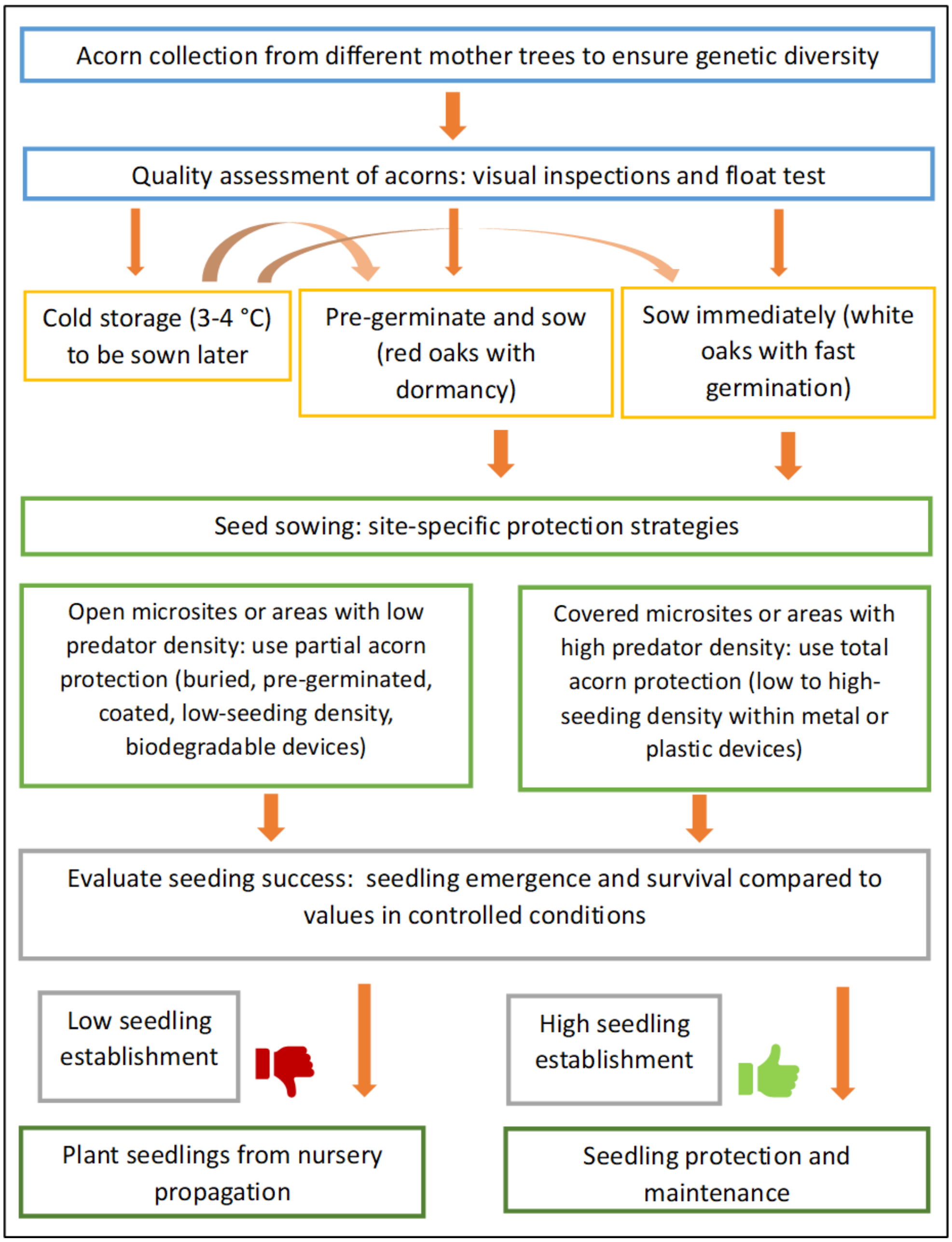

Figure 5. Diagram showing progression of the general steps for seeding acorns. For acorn collection, a minimum of five mother trees is recommended. Figures 2 and 4 show examples of total and partial protection of acorns. Low seeding density or seeding a single acorn per sowing spot and covered by plant litter reduce the probability of encounter by predators.

7 Successful seeding

7.1 Defining success

We measured seeding success by evaluating germination percentage and seedling emergence in the field (Figure 6b and 6c) relative to values recorded under controlled conditions in the nursery (Figure 6a). Results from various studies at the prior mentioned study sites are summarized in Tables 1 and 2. As general trends, we found that: (1) microsites with lower vegetative cover reduce acorn predation without affecting germination and seedling emergence; (2) when acorns are completely protected (total exclusion), germination and seedling emergence are highest (54% and 22.5%, respectively), while unprotected seed had the lowest values of these variables (12.5% and 3.5%, respectively); (3) higher acorn predation (and therefore lower germination) was recorded during non-mast years when seeding was conducted in secondary forests having canopy oaks; and (4) there is high intra- and interspecific variability in acorn mass, and also germination and seedling emergence even under controlled conditions.

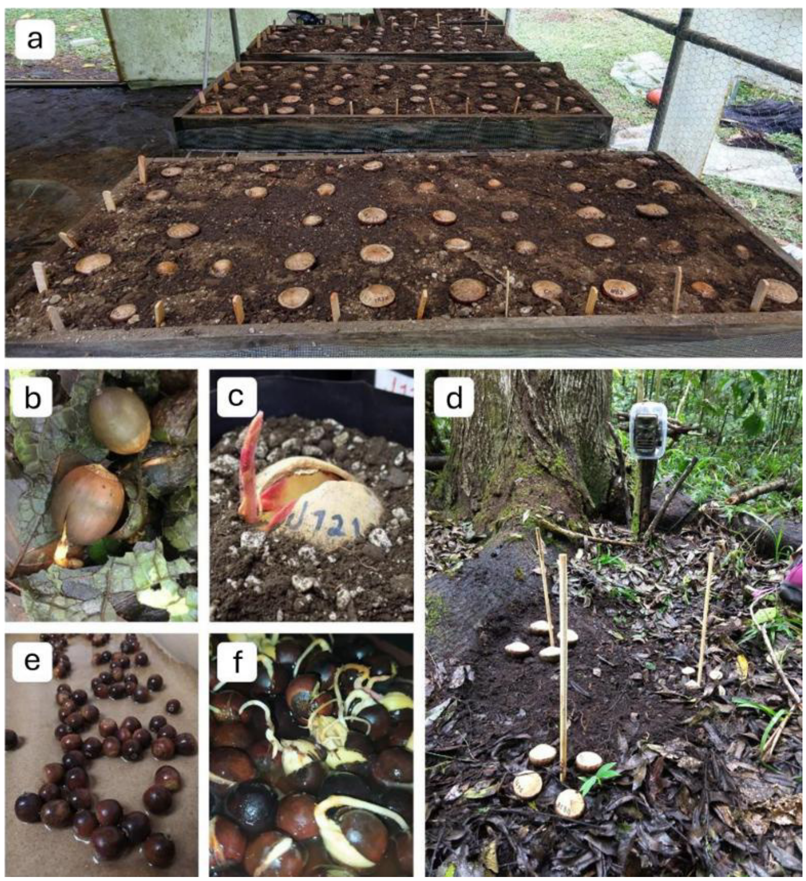

Figure 6. (a) *Quercus insignis* M. Martens & Galeotti acorns sown in a greenhouse to evaluate viability under controlled conditions. (b) Germinated acorns of *Q. sartorii* Liebm. on the forest floor. (c) *Q. insignis* seedling emergence. (d) Installation of camera trap to identify the fauna that consume *Q. insignis* acorns. (e-f) Pre-germination process for acorns of *Q. xalapensis* Bonpl. before sowing (burying) in the field (Photo credits: (a–d) Ma. de los Ángeles García-Hernández, (e–f) Dulce C. Vivar-Vázquez).

In addition, species differ in viability (acorn germination and seedling emergence) and rodent selection pressure (Tables 1 and 2). For instance, at Site 1, *Q. germana* exhibited the highest germination percentage in the field, followed by *Q. lancifolia*, *Q. xalapensis*, and *Q. sartorii*; while emergence was highest in *Q. lancifolia*, followed by *Q. xalapensis*, *Q. germana*, and *Q. sartorii*. For some species, these values were between 8 to 38.5 times lower than those recorded in greenhouse studies (Table 2). These differences could be due to species-specific removal preferences of rodents (García-Hernández et al. 2024). *Q. insignis* is highly variable in acorn mass (10 to 86 g), but these heavy acorns were also removed and consumed (Table 1); only 13.5% germinated and 0.5% emerged as seedlings in a mast year. The large size of its seed indicates a high nutrient content, so they are frequently removed by seed predators (mainly squirrels) and their establishment at planting microsites was low (García-Hernández et al. 2025). This emphasizes a regeneration bottleneck in degraded forests for some oak species and the need to plant seedlings or saplings rather than sow seed in some restoration settings.

7.2 Limiting factors and risks

We identified the bottlenecks to seedling establishment. We have also observed intra- and interspecific variability in the responses of the *Quercus* genus, as well as spatial (sowing microsites and predator assemblage) and temporal (mast years, predator population size, climatic events) heterogeneity. This variability limits the possibility of creating universally applicable protocols to successfully restore TMCF through seeding. Establishing rapid, small-scale pilot experiments and acorn availability surveys in forested areas can provide insight and reduce risk prior to implementing a large-scale program. Mast years will provide a sufficient quantity and quality of acorns to evaluate the use of pre-germinated buried acorns of different species (highest diversity) at open microsites (Figure 5). These rapid surveys allow the practitioner to decide if total or partial seed protection is needed to prevent acorn predation and seedling herbivory. Moreover, seeding density can be assessed experimentally, using 1 to 5 acorns per sowing spot to help determine and measure the probability of seed predation. Camera traps set at seeding microsites can inform the practitioner of likely seed predators (Figure 6d), which will contribute to selection of appropriate protection devices for seed and seedlings, at least for the first (establishment) year. We found that sowing unprotected seed limited establishment, with only 2.5% or fewer exposed seed reaching the seedling stage. In contrast, completely protecting seed increased seedling emergence by up to 20%.

7.3 Key elements contributing to success

Knowing the time required for germination and emergence of the various red and white oak species and the particular threats that seeds are exposed to at each site are vital for the effective design and implementation of seeding projects. Where information is not available, probable germination rates can be inferred from Section (red or white oaks) and from rapid greenhouse tests of viability. Another strategy could be to collect seed germinating in the field under mother trees (Figure 6b) because many of the seedlings in this situation will be unable to establish under the dense shade of the canopy. However, such extractions should not remove all mast because of the value of the cohort to regeneration and local fauna.

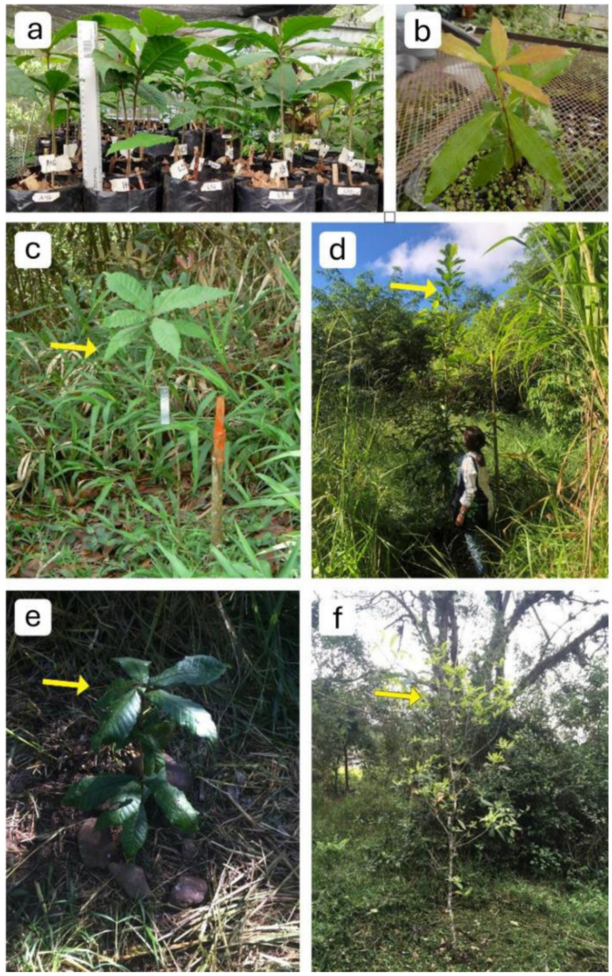

Figure 7. (a–b) Seedlings of *Q. insignis* M. Martens & Galeotti and *Q. lancifolia* Schltdl. & Cham. six months after being sown under nursery conditions. (c) 2-year-old sapling of *Q. insignis* at Site 3. (d) 4-year-old sapling of *Q. germana* Schltdl. & Cham. at Site 2. (e) 1-year-old seedling of *Q. germana* at Site 2. (f) 4-year-old sapling of *Q. pinnativenulosa* C.H.Mull. at Site 2. (Photo credits: (a–b) Ma. de los Ángeles García-Hernández, (c–f) Fabiola López-Barrera).

The five species we studied differed in the amount of time required for germination and emergence and would thus require different periods of seed protection (Table 2). The acorns of *Q. lancifolia* and *Q. xalapensis* presented late germination and emergence, and their seeds remained viable until the end of the experiment (184 days), with removal by predators resultantly continuing through this period. For these species, it is necessary that seed is sown with some type of protection or that it is pre-germinated prior to sowing (Rodríguez-Zambrano 2024). Acorns of *Q. sartorii* and *Q. germana* showed rapid germination; however, it was observed that their seeds quickly lose moisture when exposed to field conditions. Moisture loss has been related to acorn size (large cotyledons typically dry slower), acorn moisture at the time of dispersal, and pericarp condition following dispersal. Once cracked, the pericarp facilitates the process of water absorption and loss (Kang et al. 2023). In the case of *Q. insignis*, acorns presented rapid germination and emergence, but rodents were observed to cut the radicles, which prevented seedling development. It is important to consider that germination and emergence, even within the same species and regardless of Section, may vary each year due to provenance and genetic characteristics of mother trees, climatic conditions (temperature, wind, precipitation, etc.), and environmental conditions (vegetation characteristics, competition, soil nutrition, etc.) of the restoration site.

It is necessary to reverse the degradation and loss of TMCF and sustain the great diversity of foundational oaks in the region. Restoration of oaks, because of their favorable acorn characteristics, are generally quite suited to establishment with seeding. Primary issues with oak seeding in the TMCF stem from seed predation. Opportunities exist for innovating acorn protection with local materials that are inexpensive, easily installed, and biodegradable. To be successful, the design of innovative protection devices will need to account for the behaviors of main seed predators active in the region and the length of time protection is required to obtain seedling establishment.

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CAUTION

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

9 References

Baraloto C, Forget PM, Goldberg DE (2005) Seed mass, seedling size and neotropical tree seedling establishment. J Ecol 93:1156–1166. https://doi.org/10.1111/j.1365-2745.2005.01041.x

Bartlow A, Agosta S, Curtis R, Yi X, Steele M (2018) Acorn size and tolerance to seed predators: the multiple roles of acorns as food for seed predators, fruit for dispersal and fuel for growth. Integr Zool 13:251–266. https://doi.org/10.1111/1749-4877.12287

Brewster-Salmones E, Díaz-García JM, López-Barrera F (2024) Spicing up oak forest restoration: a preliminary report of the protective use of chili peppers in direct seeding of acorns. Restor Ecol 32:e14146. https://doi.org/10.1111/rec.14146

Castro J, Leverkus AB, Fuster F (2015) A new device to foster oak forest restoration via seed sowing. New For 46: 919–929. https://doi.org/10.1007/s11056-015-9478-4

CONABIO (2010) El Bosque Mesófilo de Montaña en México: Amenazas y Oportunidades para su Conservación y Manejo Sostenible. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico DF, Mexico.

Cotler H, Garrido A, Bunge V, Cuevas ML (2010) Chapter 6-Las cuencas hidrográficas de México: priorización y toma de decisiones. In: Cotler H (ed) Las cuencas hidrográficas de México: diagnóstico y priorización. Instituto Nacional de Ecología, Fundación Gonzalo Río Arronte I.A.P., Ciudad de México, México, pp 210–215.

Foster P (2001) The potential negative impacts of global climate change on tropical montane cloud forests. Earth-Sci Rev 55:73–106. https://doi.org/10.1016/S0012-8252(01)00056-3

García-de la Cruz Y, López-Barrera F, Ramos-Prado JM (2016) Germination and seedling emergence of four endangered oak species. Madera y Bosques 22:77–87. https://doi.org/10.21829/myb.2016.2221326

García-Hernández MA, López-Barrera F, Vásquez-Reyes VM (2016) Microhabitat affects acorn removal in three sympatric and endangered Neotropical oak species. Ecol Restor 31:343–351. https://doi.org/10.1007/s11284-016-1342-2

García-Hernández MA, López-Barrera F, Perea R (2023) Simulated partial predation on the largest-seeded oak: Effects of seed morphology and size on early establishment. For Ecol Manag 534:120863. https://doi.org/10.1016/j.foreco.2023.120863

García-Hernández MA, López-Barrera F (2024) Direct seeding success of four threatened oak species in a peri-urban forest: effects of microhabitat and rodent exclusion. For Ecol Manag 553:121629. https://doi.org/10.1016/j.foreco.2023.121629

García-Hernández MA, López-Barrera F, Sosa VJ, Pérez-Ramos IM, Perea R (2025) Acorn dispersal effectiveness after 27 years of passive and active restoration in a Neotropical cloud forest. Sci Total Environ 966:178770. https://doi.org/10.1016/j.scitotenv.2025.178770

Gómez Díaz JA, Lira-Noriega A, Villalobos F (2023) Expanding protected areas in a Neotropical hotspot. Int J Sustain Devel World Ecol 30:485–499. https://doi.org/10.1080/13504509.2022.2163717

Gómez-Díaz JA, Brast K, Degener J, Krömer T, Ellis E, Heitkamp F, Gerold G (2018) Long-term changes in forest cover in Central Veracruz, Mexico (1993–2014). Trop Conserv Sci 11:1–12. https://doi:10.1177/1940082918771089

Gribko LS, Jones WE (1995) Test of the float method of assessing northern red oak acorn condition. Tree Plant Notes 46:143–147.

Jiménez-García D, Peterson AT (2019) Climate change impact on endangered cloud forest tree species in Mexico. Revista Mexicana de Biodiversidad 90: e902781. https://doi.org/10.22201/ib.20078706e.2019.90.2781

Kang H, Jaganathan GK, Han Y, Li J, Liu B (2023) Revisiting the pericarp as a barrier restricting water entry/loss from cotyledons and embryonic axis of temperate desiccation-sensitive *Quercus* acorns. Planta 257:33. https://doi.org/10.1007/s00425-022-04061-4

Leverkus AB, Castro J, Puerta-Piñero C, Benayas JR (2013) Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. Ecol Eng 53:15–22. https://doi.org/10.1016/j.ecoleng.2013.01.003

Leverkus AB, Rojo M, Castro J (2015) Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing. Ecol Eng 83:276–280. https://doi.org/10.1016/j.ecoleng.2015.06.033

Liu L, Tu Y, Li Q, Deng M (2024) Seed germination characteristics of a critically endangered evergreen Oak—*Quercus marlipoensis* (Fagaceae) and their conservation implications. Forests 15:235. https://doi.org/10.3390/f15020235

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. For Ecol Manag 448:474–489. https://doi.org/10.1016/j.foreco.2019.06.032

López-Barrera F, Manson RH, González-Espinosa M, Newton AC (2007) Effects of varying forest edge permeability on seed dispersal in a neotropical montane forest. Landsc Ecol 22:189–203. https://doi.org/10.1007/s10980-006-9020-3

Montes-Hernández B, López-Barrera F (2013) Seedling establishment of *Quercus insignis*: A critically endangered oak tree species in southern Mexico. For Ecol Manag 310:927–934. https://doi.org/10.1016/j.foreco.2013.09.044

Ortega-Pieck A, López-Barrera F, Ramírez-Marcial N, García-Franco JG (2011) Early seedling establishment of two tropical montane cloud forest tree species: The role of native and exotic grasses. For Ecol Manag 261:1336–1343. https://doi.org/10.1016/j.foreco.2011.01.013

Reque JA, Martin E (2015) Designing acorn protection for direct seeding of *Quercus* species in high predation areas. For Syst 24:e018. https://doi.org/10.5424/fs/2015241-05632

Rodríguez-Acosta M, Coombes AJ (2020) Manual para la propagación de *Quercus*: Una guía fácil y rápida para cultivar encinos en México y América Central. Jardín Botánico Universitario de la Benemérita Universidad Autónoma de Puebla, Puebla, Mexico.

Rodríguez-Zambrano EU (2024) Ecología de la regeneración de *Quercus paxtalensis* C.H. Mull. y *Quercus pinnativenulosa* C.H. Mull., especies amenazadas del bosque de niebla. MSc Dissertation, Instituto de Ecología A C Xalapa, Mexico. 61 pp.

Rojas-Soto O, Sosa V, Ornelas J (2012) Forecasting cloud forest in eastern and southern Mexico: Conservation insights under future climate change scenarios. Biodiver Conserv 21:2671–2690. https://doi.org/10.1007/s10531-012-0327-x

Rzedowski J (1996) Análisis preliminar de la flora vascular de los bosques mesófilos de montaña de México. Acta Botánica Mexicana 35:25-44. https://doi.org/10.21829/abm35.1996.955

Salinas N, Cosio EG, Silman M, Meir P, Nottingham AT, Roman-Cuesta RM, Malhi Y (2021) Tropical montane forests in a changing environment. Front Plant Sci 12:712748. https://doi.org/10.3389/fpls.2021.712748

Steele MA, Smallwood PD, Spunar A, Nelsen E (2001) The proximate basis of the oak dispersal syndrome: detection of seed dormancy by rodents. Am Zool 41:852–864. https://doi.org/10.1093/icb/41.4.852

Steele MA (Ed) (2021) Oak seed dispersal: a study in plant-animal interactions. Johns Hopkins University Press, Baltimore, MD, USA.

Schroeder W, Walker D (1987) Effects of moisture content and storage temperatures on germination of *Quercus macrocarpa* acorns. J Environ Hortic 5:22–24. https://doi.org/10.24266/0738-2898-5.1.22

Toledo-Aceves T, Meave JA, González-Espinosa M, Ramírez-Marcial N (2011) Tropical montane cloud forests: current threats and opportunities for their conservation and sustainable management in Mexico. J Environ Manag 92: 974–981. https://doi.org/10.1016/j.jenvman.2010.11.007

Toledo-Aceves T (2017) Germination rate of endangered cloud forest trees in Mexico: potential for ex situ propagation. J For Res 22:61-64. https://doi.org/10.1080/13416979.2016.1273083

Toledo-Aceves T, Guariguata MR, Günter S, Porter-Bolland L, Merino L (2021a) Overcoming key barriers for secondary cloud forest management in Mexico. Land 10:1078. https://doi.org/10.3390/land10101078

Toledo-Aceves T, Trujillo-Miranda AL, López-Barrera F (2021b) Tree regeneration in active and passive cloud forest restoration: Functional groups and timber species. For Ecol Manag 489:119050. https://doi.org/10.1016/j.foreco.2021.119050

Toledo-Aceves T, López-Barrera F, Vásquez-Reyes V, Günter S (2022) Restoration of tropical montane cloud forest in bracken dominated pastures: The role of nurse shrubs. For Ecol Manag 508:120055. https://doi.org/10.1016/j.foreco.2022.120055

Trujillo-Miranda AL, Toledo-Aceves T, López-Barrera F, Gerez-Fernández P (2018) Active versus passive restoration: Recovery of cloud forest structure, diversity and soil condition in abandoned pastures. Ecol Eng 117:50–61. https://doi.org/10.1016/j.ecoleng.2018.03.011

Vander Mijnsbrugge K, Bischoff A, Smith B (2010) A question of origin: where and how to collect seed for ecological restoration. Basic Appl Ecol 11:300–311. https://doi.org/10.1016/j.baae.2009.09.002

Williams-Linera G (2012) El bosque de niebla del centro de Veracruz: ecología, historia y destino en tiempos de fragmentación y cambio climático. CONABIO-Instituto de Ecología A C, Xalapa, Veracruz, Mexico.

Williams-Linera G, Toledo-Garibaldi M, Gallardo Hernández C (2013) How heterogeneous are the cloud forest communities in the mountains of central Veracruz, Mexico? Plant Ecol 214:685–701. https://doi.org/10.1007/s11258-013-0199-5

Williams-Linera G, López-Barrera F, Bonilla-Moheno M (2015) Establishing the baseline for cloud forest restoration in a peri-urban landscape. Madera y bosques 21:89–101.

Seeding bottomland oaks (*Quercus* spp.) in the southern United States

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Abstract

Temperate broadleaf forests occupying river floodplains of the southern United States are rich in tree species diversity, with various species of bottomland oaks (*Quercus* spp. L.) often comprising a primary overstory component in these forests across the region. Comprehensive research to support development of seeding as a method for artificially regenerating bottomland oaks began in the early 1980s and quickly advanced to produce reliable practices for establishing oak-dominated stands. Large-scale forest restoration was initiated across the region during the late 1980s at which time bottomland oak seeding practices were adapted for broad scale use due to their relatively low costs. This manuscript presents a synthesis of basic bottomland oak ecology, factors leading to degradation of bottomland oak sites and stands, favored techniques and practices for restoring bottomland oak forests through seeding, factors that limit success and impose risks upon seeding projects, and silvicultural principles for seeding bottomland oaks in the southern United States.

Keywords

forest restoration, afforestation, direct seeding, *Quercus*

Contents

1 The forest

Bottomland forests of the southern United States occur on floodplains and terraces of the numerous major and minor river systems that dissect the Atlantic and Gulf Coastal Plain of the region (Figure 1). Today, these deciduous broadleaf forests are recognized for providing a multitude of ecosystem services including wood products, water quality, recreation, floodwater abatement, carbon sequestration, fish and wildlife habitat, and many others that sustain livelihoods in the southern US and beyond. Historically, though, bottomlands were recognized for their fertile soils, and incentives for growing the agricultural economy of the southern US led to incremental and wide-scale deforestation of these systems. In the case of the greatest expanse of bottomland forest, i.e., the Lower Mississippi Alluvial Valley (LMAV) (Figure 1), deforestation resulted in loss of more than 70% of this 10-million ha resource, beginning in the 1800s and continuing through the 1980s (Sternitzke 1976; MacDonald et al. 1979). Yet, the last three decades have witnessed a growing awareness of the ecological and economic value of these forested systems, and this has fostered federal government policy encouraging conservation of existing bottomland forests and funding wide-scale restoration of deforested or otherwise degraded bottomlands.

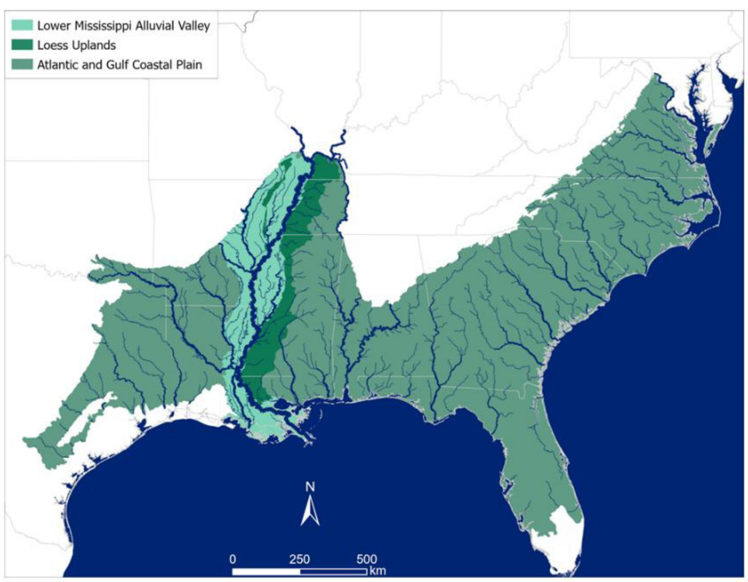

Figure 1. Map of the southern United States that outlines the Atlantic and Gulf Coastal Plain, the Lower Mississippi Alluvial Valley, and the numerous river systems that give rise to bottomlands in the region.

Prior to the wide-scale afforestation effort of the past three decades, US Forest Service scientists located in Stoneville, MS initiated comprehensive research to support development of seeding as a practice for artificial regeneration of bottomland oaks

(Johnson and Krinard 1985). Their success in advancing seeding as a viable practice for establishing bottomland oaks on former agricultural land led to its early use on many state and federal wildlife management areas and refuges where restoration of bottomland forests first received wide-scale adoption (Allen 1990). At that time, the nursery capacity to produce bottomland oak seedlings was low and seeding provided a relatively inexpensive and low intensity approach for large-scale establishment of bottomland oak stands. With the advancement of forest restoration and improved knowledge of bottomland oak stand development, restoration managers now promote establishment of mixed, bottomland oak stands, i.e., stands comprised of 25–50% bottomland oak with the remainder being other native tree species. Most of the trees naturally occurring with bottomland oaks are light seeded and proper techniques for seeding them have not been developed, so seeding to establish stands of bottomland oak has fallen out of favor. Nevertheless, there are particular restoration settings in which seeding remains a low-cost, viable practice for establishing bottomland oaks on deforested agricultural land, and work on acorn biology and storage, estimating soil productivity, site preparation requirements, and sowing practices conducted by those early scientists serves as the foundation for many of the techniques and practices that will be presented later in this manuscript.

1.1 Bottomland environments

Structure and productivity of bottomland forests are inextricably coupled to the site factors that prevail on floodplains. Although seemingly homogeneously flat to the casual observer, scouring and deposition of alluvium associated with annual overbank flooding and meandering of the river channel create significant topographic relief giving rise to landforms or "sites" and development of their associated soils (Figure 2). About six general sites characteristic of floodplains and terraces of the southern US are distinguished by topography, soil physical and chemical properties, and hydrologic regime (Hodges 1997). Soil development for a site progresses relative to the physical and chemical properties of its alluvium, time since deposition, position on the landscape, and other factors of environment and climate including vegetation and hydrologic regime. Entisols, Inceptisols, Alfisols, and Vertisols prevail on floodplains, partly because of the recency of alluvial deposition; Alfisols, Ultisols, and Vertisols prevail on terraces where deposition no longer occurs, and soil development has advanced (Stanturf and Schoenholtz 1998; NRCS 2020).

A temperate climate prevails over the bottomlands of the southern US—it is primarily humid, sub-tropical with cool winters and warm to hot summers (Muller and Grymes 1998). Precipitation is generally high, ranging between 1059 and 1609 mm annually, while the average daily temperature ranges from 0 to 12.4 °C in January to 22.0 to 28.8 °C in July (NOAA 2023). Although forecasts are plagued with uncertainty, temperature and rainfall patterns are expected to differ in the future across the southern US. Estimates through 2060 indicate that average annual temperatures could rise by 1 to 2.9 °C across the Coastal Plain and LMAV portions of the region, with greatest increases generally farthest from coastlines of the Atlantic Ocean and the Gulf of America. Precipitation forecasts through 2060 are variable and range between a 5% increase to an 18% decrease, annually, for the focal area. Increasing precipitation is most likely near the coastlines while decreasing precipitation is most likely interior from the coastlines (McNulty et al. 2013).

Figure 2. Image of the Pearl River and an area of its floodplain in Mississippi, USA illustrating erosion on the outer edge of bends, deposition on the inside of bends, and older meander scars which give rise to and are indicative of the various sites that are characteristic of floodplains and terraces of bottomlands in the southern US.

1.2 Native forests and bottomland oak ecology

In respect to temperate forests, the deciduous broadleaf forests of bottomlands are notably rich in tree species diversity with over 75 indigenous species occurring in these riverine habitats across the southern US. Species that are widespread in bottomlands throughout the region include sweetgum (*Liquidambar styraciflua* L.), green ash (*Fraxinus pennsylvanica* Marshall), boxelder (*Acer negundo* L.), sugarberry (*Celtis laevigata* Willd.), American elm (*Ulmus americana* L.), eastern cottonwood (*Populus deltoides* Bartram ex Marshall), black willow (*Salix nigra* Marshall), American sycamore (*Platanus occidentalis* L.), baldcypress (*Taxodium distichum* (L.) Rich.), water tupelo (*Nyssa aquatica* L.), hickories (*Carya* spp. Nutt.), and oaks (*Quercus* spp. L.). Midstory and understory strata naturally develop in some bottomland forest associations: small trees regularly found in midstories include American hornbeam (*Carpinus caroliniana* Walter), maples (*Acer* spp. L.), hollies (*Ilex* spp. L.), and hawthorns (*Crataegus* spp. Tourn. ex L.); common understory woody shrubs include northern spicebush (*Lindera benzoin* L.), common sweetleaf (*Symplocos tinctoria* (L.) L'Her.), snowbells (*Styrax* spp. L.), and American beautyberry (*Callicarpa americana* L.); and large, perennial monocots of frequent occurrence in understories include giant cane (*Arundinaria gigantea* (Walter) Muhl.) and palmetto (*Sabal minor* (Jacq.) Pers.). Also, with more than 25 indigenous species, bottomland forests are rich in woody vines; ubiquitous species include poison ivy (*Toxicodendron radicans* (L.) Kuntze), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.), Alabama supplejack (*Berchemia scandens* (Hill) K. Koch), crossvine (*Bignonia capreolata* L.), grapes (*Vitis* spp. L.), and greenbriers (*Smilax* spp. L.).

Collectively, the oaks often comprise a primary overstory component in bottomland forests—as many as 17 species can be found in bottomlands, 10 of which are common to these forests across the region (Table 1). Seven of the species common to bottomlands are in the section Lobatae, the red oaks, and three are in the section Quercus, the white oaks. In bottomlands, oaks grow in association with other canopy species and these associations are found segregated among different site types (Hodges 1997) (Table 1). Thus, the occurrence of the various oak species in bottomland forests, and their primary co-occurring species, is largely predicated upon the area occupied by the various site types. Driving species-site associations in bottomlands are soil and hydrologic factors inherent to the scope of bottomland sites, e.g., soil flooding and soil pH, along with physiological tolerances and functional plasticities inherent to the various tree species. Distinctly, the range in flood tolerance among bottomland oaks plays a central role in distribution and stratification of the various species on the floodplain.

Table 1. Silvical characteristics of 10 oak species common to bottomlands of the southern US.

Species	Soil and Site Occurrence[1]	Seedling Flood Tolerance[2]	Seedling Shade Tolerance[3]	Seedling Growth Rate[4] (cm per year)
		Section Quercus		
Overcup oak (*Q. lyrata* Walter)	Poorly drained, clayey soils of low flats, sloughs, and other depressions on floodplains and terraces	Tolerant	Moderately Tolerant	15–25
Swamp chestnut oak (*Q. michauxii* Walter)	Well drained, loamy soils of low ridges on terraces, less common on floodplains	Moderately Intolerant	Moderately Intolerant	15–25
White oak (*Q. alba* L.)	Well drained, loamy soils of ridges, principally on terraces	Intolerant	Tolerant	15–25
		Section Lobatae		
Cherrybark oak (*Q. pagoda* Raf.)	Well drained, loamy soils of ridges and high flats on floodplains and terraces	Moderately Intolerant	Intolerant	15–25
Nuttall oak (*Q. texana* Buckley)	Poorly drained, clayey soils of flats and low ridges on floodplains and less commonly terraces	Moderately Tolerant	Intolerant	20–30
Pin oak (*Q. palustris* Münchh.)	Poorly drained, clayey soils of flats and low ridges on floodplains and terraces	Moderately Tolerant	Moderately Intolerant	15–25
Water oak (*Q. nigra* L.)	Poorly drained, clayey soils of low flats to well drained, loamy soils of ridges and high flats on floodplains and terraces	Moderately Intolerant	Moderately Intolerant	10–20
Willow oak (*Q. phellos* L.)	Poorly drained, silty or clayey soils of low flats to well drained, loamy soils of ridges and high flats on floodplains and terraces	Moderately Tolerant	Moderately Intolerant	15–25

Shumard oak (*Q. shumardii* Buckley)	Well drained, loamy soils of ridges on terraces and less commonly floodplains	Intolerant	Intolerant	15–25
Swamp laurel oak (*Q. laurifolia* Michaux)	Poorly drained, clayey soils of low flats and borders of sloughs on floodplains	Moderately Tolerant	Moderately Tolerant	10–20

[1] Putnam and Bull (1932).
[2] Seedling flood tolerance rankings are based on unpublished observations of the authors and are relative to the bottomland oaks.
[3] Based on shade tolerance rankings of mature trees presented in Burns and Honkala (1990) that were modified for seedlings relative to unpublished observations of the authors.
[4] Based on seedling growth information presented in Burns and Honkala (1990), Miwa et al. (1993) and Gardiner et al. (2004) that was modified by the authors to bracket seedling growth during the first 5 years after germination for afforestation sites that receive no post-sowing competition control.

The occurrence of bottomland oaks on the floodplain is also predicated upon the disturbance regime of a given site. As bottomland oaks are largely shade intolerant (Table 1), development of oak associations on favorable sites is facilitated where major canopy disturbance (stand replacing) has occurred (Oliver et al. 2005). Floodwater inundation and significant wind events are among the most common natural disturbance factors impacting bottomland forests. Seasonal flooding of bottomlands rarely impacts the overstory and midstory of mature forests but can affect understory vegetation including the oak regeneration pool. Long-term inundation from impoundment of water by beaver (*Castor canadensis*) or deposition of sediment and debris that blocks the flow of floodwater through return channels more commonly create major canopy disturbance attributable to flooding in bottomlands. High winds from hurricanes regularly impact bottomland forests near coastlines, and tornados impose stand-replacing impacts locally across the region (Cannon et al. 2023; Stanturf et al. 2007).

Bottomland oak stands tend to occur in mid-successional seres that follow major canopy disturbance to stands dominated by early successional species like eastern cottonwood, black willow, river birch, boxelder, American sycamore, American elm, and green ash (Hodges 1995). But it is not uncommon for stands of bottomland oak and sweetgum to occur in an early-successional sere in situations of old field abandonment, or for stands of bottomland oak and hickories to occur in a late-successional sere on sites that no longer receive flooding. Bottomland oak stands typically “mature” in 45 to 60 years, and their canopies begin to break up around years 100 to 150 (Kennedy and Nowacki 1997). Depending on species composition and site productivity, basal area of mature stands will range from 20 to 43 m^2 ha^{-1} and canopy height will range from 26 to 38 m (Meadows and Nowacki 1996; Kennedy and Nowacki 1997).

1.3 Deforestation and afforestation of bottomlands

Deforestation of bottomlands in the southern US began in earnest after substantial settlement of the region in the 1700s and increased incrementally through the 1980s. Estimates indicate that forest area of the LMAV, which has experienced the most widespread deforestation of bottomland in the region, was reduced to 50% of its original 11-million-ha extent by the 1930s, and to more than 75% of its original extent by the 1970s (MacDonald et al. 1979). Most of the historical deforestation was driven by expansion of the agricultural sector in the region which was supported by federal drainage and flood control projects. In recent decades, clearing for agriculture has been somewhat limited by US government “Swampbuster” legislation enacted in 1985, particularly on sites classified as wetlands (Stanturf et al. 2000). During this time, incentives established through additional US government legislation have promoted the afforestation of economically marginal and highly erodible agricultural land. Forest restoration in the LMAV, for example, has afforested well beyond 400,000 ha of former agricultural land since the 1990s (Gardiner 2014). Nevertheless, deforestation of bottomlands continues to persist across the region as development of rural areas and urban expansion progress with a growing population (Gardiner 2014).

2 Impacts of deforestation to bottomland sites

2.1 Site and soil degradation

Restoration in alluvial bottomlands of the southern US is practiced almost exclusively on former agricultural land. Deforestation and conversion to farming land use impose significant soil disturbance, alter natural hydrologic regimes, and affect species composition of colonizing vegetation at bottomland restoration sites. Major impacts of cultivation on bottomland soils include heightened erosion, the loss of organic matter, development of traffic pans, impairment of soil drainage (surface and internal), reduced soil fertility, and shifts in the soil microbial community (Groninger et al. 2000; Stanturf et al. 2004; Strickland et al. 2017). Too, the hydrologic regime of farmed bottomlands is significantly altered from the natural state. Depending on the setting of the restoration area on the landscape and occurrence of bottomland site types on the area, common impacts to the hydrologic regime will involve shifts in timing, duration, and depth of soil flooding, change in soil water retention, and an increased depth to the water table (Stanturf et al. 2004; Ouyang et al. 2019). Further, changes in colonizing plants typically reveal communities that are characteristic of old fields rather than bottomland forests, often with a preponderance of invasive weeds like Johnsongrass (*Sorghum halepense* (L.) Pers.), Brazilian vervain (*Verbena brasiliensis* Vell.), and Wright’s morning-glory (*Ipomea wrightii* Sweet) that flourish in agricultural settings (Battaglia 2002; DeSteven et al. 2015). Collectively, the degradation of edaphic, hydrologic, and vegetative factors disrupts nutrient, carbon, and water cycling functions of the site, leading to reduced productivity and curtailment of many other ecosystem functions attributed to bottomland systems.

Because site and soil degradation impair forest establishment, reduce site productivity, and ultimately jeopardize restoration success of bottomland forests, it is helpful for the manager to accurately assess the extent of degradation to inform the restoration prescription. This will reveal issues that should be mitigated to facilitate recovery of the site and soil functions. An evaluation of the relative extent of site degradation can be approached by compiling information on key variables from the restoration site and adjacent properties. Important observations to collect include those that index the extent of constructed drainage and dikes, leveling of topography through land-forming, recent history of flooding, length of time in agriculture, and occurrence of invasive or otherwise problematic weeds. Likewise, the relative extent of soil degradation should be characterized through measurement of key variables that index the status of soil organic matter content, soil compaction, soil nutrient pools, and soil aeration. Baker and Broadfoot (1979) provide a simple field tool for assessing site productivity of bottomland soils—their tool relies on quantification of variables descriptive of soil physical condition, moisture availability, nutrient availability, and aeration (Table 2). Groninger et al. (2000) provide updated recommendations for application of the Baker and Broadfoot guide to sites degraded by cultivation.

2.2 Damaging agents

Several biotic and abiotic factors, which act through depredating sown acorns, impairing acorn viability, suppressing early seedling growth, or causing seedling mortality, can threaten success of bottomland oak seeding on former agricultural land. Insect pests and pathogenic diseases generally pose minimal impact to establishment and early growth of bottomland oaks on restoration sites. Mammals, especially feral pigs (*Sus* spp.), racoons (*Procyon lotor*), and rodents (Order Rodentia) like mice, rats (Suborder Myomorpha), and squirrels (Suborder Sciuromorpha), relish acorns and are known to systematically search for and depredate those sown on restoration sites. Rodents and rabbits (*Sylvilagus* spp.) commonly feed on young oak seedlings—their girdling of bark or stem clipping is often not lethal because bottomland oak seedlings possess the ability to resprout if the root collar remains intact (Figure 3). This feeding activity does, however, reduce seedling vigor and delays seedling recruitment into a larger size class, both of which hold the reproduction in a size class vulnerable to repeated herbivory and other threats. Herbivory by voles (*Microtus* spp.) will often kill seedlings because of their belowground feeding on the root system. White-tailed deer (*Odocoileus virginianus*) do not pose a widespread browsing issue on restoration sites of southern bottomlands, but they may present local issues where restoration is sited proximally to urban greenspace.

Table 2. List of diagnostic variables for four major site and soil factors employed by Baker and Broadfoot (1979) to assess productivity of bottomland soils.

Site and soil Factor	Diagnostic Variables
Soil Physical condition	Soil depth, presence of pans (artificial or inherent), soil texture, soil compaction, soil structure, past land use
Moisture availability	Water table depth, presence of pans (artificial or inherent), position on the landscape, microsite topography, soil structure, soil texture, occurrence of flooding, past land use
Nutrient availability	Geologic source of parent material, past land use, % soil organic matter, topsoil depth, soil age, soil pH
Aeration	Soil structure, swampiness, soil color, presence of mottling

Figure 3. Water oak (*Q. nigra* L.) seedling that has resprouted after being clipped multiple times by a rabbit (*Sylvilagus* spp.). Clipping reduces seedling vigor and delays stem development, which increases seedling vulnerability to additional clipping, competing vegetation, and floodwater inundation (Photo credits: Emile Gardiner).

Dense and vigorous old field vegetation that typically develops on afforestation sites can pose challenging risks to establishment and early growth of seeded bottomland oaks. Invasive grasses like Johnsongrass, and itchgrass (*Rottboelllia cochinchinensis* (Lour.) Clayton), herbaceous broadleaves like Brazilian vervain, asters (*Aster* spp. L.), and goldenrods (*Solidago* spp. L.), and aggressive vines like trumpet creeper (*Campsis radicans* (L.) Bureau), red vine (*Brunnichia ovata* (Walter) Shinners), and blackberry (*Rubus* spp. L.) quickly capture growing space then overtop and out-compete the characteristically slower-growing oak seedlings. Competition from dense vegetation during the establishment period will directly reduce seedling survival and it also delays oak seedling development, which increases vulnerability to herbivory and overtopping by floodwater.

Seasonal flooding drives ecological function of natural bottomland systems, and the acorns and seedlings of bottomland oaks are adapted to tolerate some soil flooding. Still, site inundation and soil waterlogging can adversely impact the afforestation effort when timing is unseasonable, duration is prolonged, or floodwater is too deep. Acorns, especially of the section Lobatae, sown during the dormant season will typically remain dormant for several months in waterlogged soil. In this situation, acorn viability remains intact, and germination will proceed when floodwater recedes, and aerobic conditions prevail in the soil. However, if soil waterlogging persists into warmer months, the acorns of some bottomland oaks will rot under the warm, anaerobic soil conditions. An exception to this occurrence is observed in overcup oak (*Q. lyrata* Walter), a species with acorns well-adapted for hydrochory. Acorn viability for this species has been observed to persist on inundated sites into the late summer or early fall. In natural bottomland systems, this phenomenon appears partly tied to the fact that overcup oak acorns float and thus may avoid anerobic conditions beneath floodwater. But observation of late-season germination by acorns buried under debris or sediment indicates other mechanisms may contribute to viability maintenance in this species.

The ability of bottomland oak seedlings to survive soil waterlogging or inundation varies by species and is also affected by seedling phenology, age, and size (Table 1). Flood tolerance rankings assigned to bottomland oaks generally refer to the ability of a species to tolerate soil waterlogging rather than inundation. As noted in Table 1, seedling tolerance to soil waterlogging ranges considerably by species. Oaks that regularly occur on lower elevation sites of heavier soils tend to exhibit greater tolerance to soil waterlogging than those regularly found on higher elevation sites of loamier soils. However, tolerance to soil waterlogging is also conditioned by seedling phenology, timing, and duration of anaerobic soil conditions.

For all bottomland oaks, flooding that overtops recent germinants for more than a very brief period, perhaps no more than a few days, will almost always be lethal. Likewise, mortality can advance quickly for actively growing seedlings overtopped by unseasonable floodwater during the hot months of summer. In contrast, seedlings of some species will survive overtopping for up to two months if site inundation occurs during the dormant period of the cool winter months. In this situation, cool, flowing water reduces the impact of inundation on established seedlings.

3 Mitigating impacts for seeding

3.1 Preparing the site

As indicated above, forest restoration in alluvial bottomlands of the southern US is practiced almost exclusively on sites degraded by agriculture. The site preparation phase of the restoration process provides the first opportunity for managers to mitigate some of the site and soil degradation discussed above and facilitate initiation of recovery of bottomland forest functions. Land-forming, improving and/or removing water management structures, cultivation, sub-soil plowing, fertilization, and vegetation control represent the primary practices considered by managers developing site preparation prescriptions for bottomland sites.

Land-forming is an engineering practice that is used when it is necessary to return spatial heterogeneity of topographic relief to the degraded restoration site (Figure 4). Topographic relief is important for encouraging hydroperiods more naturally associated with the suite of soil series present on the area. For example, raising surface elevations to form ridge features over soil series that are loamy in texture or lowering surface elevations to form depressions in soil series that are clayey in texture would pair the site-soil combinations with respective hydrologic regimes. Land-forming is a very expensive practice and is usually not necessary unless natural topographic relief of the restoration site was precision leveled during the previous farming operation. Further, restoration projects that are financially sound enough to bear the expense of land-forming would probably plant seedlings rather than sow seed to restore vegetation.

Figure 4. Land-forming a former agricultural site to restore topographic relief that was removed when the site was under cultivation (Photo credits: USDA, NRCS).

Practices more commonly used to restore hydroperiods on bottomland restoration sites include plugging of ditches to reduce surface drainage and installation of water control structures to manage temporary retention and impounding of water on-site (Figure 5). Restoring a hydrologic regime of flowing floodwater characteristic of seasonally flooded floodplains is usually an unrealistic objective on most bottomland restoration areas because of the many flood control projects that have minimized connectivity of rivers with their floodplains by constructing retainment levees and floodwater abatement reservoirs. Locally, altering drainage in low-relief landscapes could adversely impact neighboring properties. Still, capturing local precipitation on the restoration area will replace elements of the natural hydroperiod that can restore some functions of bottomland soils (Hunter et al. 2008).

Figure 5. Water control structure installed to manage water retention and wetland functions within a shallow depression on an afforestation site. Notice the saplings established in the right background where the topography grades to a higher elevation (Photo credit USDA, NRCS).

Most former agricultural sites slated for seeding will require cultivation to reduce row crop stubble or weedy vegetation and prepare the seedbed for sowing. In practice, cultivation is conducted with either a single or double pass of a disking implement—single pass disking is performed where residual crop stubble comprises most of the vegetative matter on the area, and double pass disking is performed where fields recently have not received cultivation, and weedy vegetation has occupied the site. Soils that have developed traffic pans should receive subsoil ripping after cultivation (Figure 6). Either straight shank or winged-shank subsoil plows are recommended for breaking-up traffic pans to increase the potential rooting depth for tree growth. Because subsoil plowing creates temporary, linear furrows on the restoration site, it is also beneficial for establishing rows that are sometimes desired for seeding.

Figure 6. Subsoil ripping of an afforestation site to break-up a traffic pan and increase rooting depth (Photo credits: USDA, NRCS).

Although most farmed soils in the southern US are typically nutrient deficient, e.g., nitrogen deficient, fertilization is rarely used to amend soil nutrition prior to sowing in bottomlands. Control of competing vegetation can benefit oak seedlings competing for available soil nutrients, and broadcast applications of herbicide tank mixes are a common site preparation practice for oak establishment on former agricultural sites. Herbicides commonly used for site preparation and early season control of grasses and herbaceous broadleaves include sulfometuron methyl, glyphosate, oxyfluorfen, fluazifop-P-butyl, and clethodim (Cunningham et al. 2019). Depending on weed development and composition, a single application of an appropriate tank mix is either broadcast across the entire area or applied in rows the fall before sowing season or immediately after acorns are sown.

3.2 Limiting acorn depredation and seedling damage

Acorn depredation and damage to young seedlings by feral pigs, rodents, raccoons, and rabbits can be primary factors contributing to poor stocking and delayed development of seeded bottomland oak stands on former agricultural sites. Devices designed to protect seed and seedlings from pilfering or damage, e.g., seed and seedling shelters, are not conventionally used on bottomland restoration areas because of the large scale of most afforestation projects and costs involved with their deployment and removal from the area (Löf et al. 2019). Likewise, fencing large restoration areas is usually a cost prohibitive option for controlling acorn depredation by feral pigs. Managers preparing to seed bottomland oaks should assess the current extent of vegetative cover, i.e., old field vegetation and crop stubble, on or immediately adjacent to the area. Such cover typically provides quality habitat for mice and rats and should be removed with cultivation during site preparation. Additionally, wooded edges and fallow fields that border the restoration area usually harbor racoons, squirrels and other rodents that pilfer sown acorns, so cultivation should be used to temporarily minimize connectivity between these areas and the adjoining restoration area. Acorn depredation by feral pigs can be reduced through permitted trapping to control the population.

Controlling significant rodent and rabbit damage to young seedlings is also a matter of minimizing cover on the restoration area. While cultivation is effective in clearing the area of old field vegetation in preparation for sowing, the treatment is temporary, and it does not retard the rapid development of succeeding vegetation. Sowing acorns in rows allows for additional cultivation as needed to set-back heavy vegetative cover that holds mice, rats, and rabbits. As with cultivation, herbicide applications made for site preparation also show temporary efficacy. Early season herbicide applications can further delay development of weedy vegetation on bottomland restoration areas. Herbicides commonly used to control grasses and some broadleaf weeds after acorns have germinated and seedlings are actively growing include clethodim and clopyralid (Cunningham et al. 2019).

Rabbit damage to young bottomland oak plantations is also frequently curbed through legal hunting. Rabbit hunting with beagle hounds is deeply rooted in tradition of the southern US and is a lawful and effective means for controlling rabbit population size and damage to seedlings. Areas of forest restoration on state and federal lands are usually open to the public for rabbit hunting because these lands are generally managed by a wildlife agency of the respective owner. On private property, landowners noting significant rabbit damage on their restoration areas will often invite local hunting groups to assist with control of the population.

4 Seed procurement and preparation

Acorn procurement and preparation for sowing is a critically important, active process for ensuring successful initiation of the restoration project. Procuring quality bottomland oak acorns begins with locating reproductive-aged stands of the appropriate species local to the afforestation site because few orchards for seed production exist and seed movement protocols for the future climate have not been developed. Reproductively mature bottomland oaks hold the potential to flower and produce acorns every year. For species in the section Quercus, flowering occurs in the spring and acorns complete maturation in the fall. In contrast, acorn development is suspended after pollination in the section Lobatae*,* and maturation is completed during the fall of the succeeding year. Seed collecting occurs when mature acorns are shed from the tree during the fall and early winter months—shedding varies by species within this period, which will determine when acorns of a given species can be harvested (Table

3). Heavy masting varies considerably in frequency and occurrence among species (Table 3), and its unpredictable nature often leads to limited seed availability from local stands.

Table 3. Masting and shedding characteristics of 10 oak species common to bottomlands of the southern US.

Species	Masting frequency[1] (years between heavy masting)	Acorn shedding period[2] (month)				
		Sept.	Oct.	Nov.	Dec.	Jan.
Section Quercus						
Overcup oak (*Q. lyrata* Walter)	3–4	XXXX	XXXXXXXXX			
Swamp chestnut oak (*Q. michauxii* Walter)	3–5	XXX	XXXXXXXXX			
White oak (*Q. alba* L.)	4–10	XXX	XXXXXXXXX			
Section Lobatae						
Cherrybark oak (*Q. pagoda* Raf.)	1–2		XXXX	XXXXXXXXXX	XX	
Nuttall oak (*Q. texana* Buckley)	3–4			XXXXXX	XXXXXXXX	XX
Pin oak (*Q. palustris* Münchh.)	1–2		XXXX	XXXXXXXXXX	XX	
Water oak (*Q. nigra* L.)	1–2		XXXX	XXXXXXXXXX	XX	
Willow oak (*Q. phellos* L.)	1		XXXX	XXXXXXXXXX	XX	
Shumard oak (*Q. shumardii* Buckley)	2–3		XXXX	XXXXXXXXXX	XX	
Swamp laurel oak (*Q. laurifolia* Michaux)	1		XXXX	XXXXXXXXXX	XX	

[1] Bonner (2008).

[2] Based on masting information noted in Burns and Honkala (1990) and unpublished observations of the authors.

Acorns are usually collected beneath fecund trees in bottomland oak stands by raking the nuts into piles that can be easily bagged and transported. Before raking begins, the collector should, using a small knife, cut open a small (about 10) sample of acorns to check for general condition, insect damage, and apparent viability. If the acorns appear in good quality, leaf litter is removed from the immediate area with hand-held leaf blowers, and heavier branches and other debris are moved off site. After raking the nuts into small piles, winnowing the piles with a rake and leaf blower helps remove acorn caps and other small debris before bagging and transporting the acorns to the processing and storage facility.

Upon arrival at the processing facility, the freshly collected acorns should be "float-tested" or plunged in clean water. Float-testing provides a simple technique for: separating insect damaged and desiccated nuts from the lot, cleaning fine debris and soil from the lot, and hydrating the nuts for storage. Because bottomland oak acorns are recalcitrant (i.e., they do not survive drying and freezing), they must maintain a sufficient moisture content (about 45–50% for section Quercus and 30% for section Lobatae) to retain viability in storage (Bonner and Vozzo 1987). To ensure complete hydration, the nuts should remain submerged in cool water overnight. If collections are made under wet or muddy field conditions, occasional stirring and water changes help clean the nuts for storage. Float-testing is not useful for separating sound from unsound nuts of overcup oak. The acorn of this species has a persistent cap that nearly encases the entire nut, and a corky layer surrounding the kernel that gives the acorn buoyancy—this acorn buoyancy is an adaptation that facilitates hydrochory in bottomland habitats. Still, the storage moisture status of overcup oak acorns is benefited by soaking them in clean water overnight.

Cleaned and adequately hydrated acorns should be removed from water and kept in a cool area for enough time to allow surface water to evaporate from the nuts before placing into cold storage. Refrigerated storage (1 to 3 °C) in polyethylene bags (≤ 10-mil thickness) has proven best for moderating metabolism and providing adequate gas exchange for acorns of both sections (Bonner and Vozzo 1987). Due to their recalcitrance, bottomland oak acorns do not retain viability through extended storage. In practicality, acorns of most species in the section Quercus will store for no more than 6 months, while acorns of most species in the section Lobatae will store for up to a year without substantial loss in viability (but see Bonner and Vozzo 1987). Maintaining gas exchange and moisture content are critical for retaining acorn viability during storage, so additional soaking may be required to maintain moisture status during extended storage.

Acorns of bottomland oak species in the section Quercus exhibit weak to no dormancy, often initiating germination and showing radicle extension under favorable environmental conditions soon after they shed from the tree. Acorns of species in the section Lobatae typically show a weak dormancy that is broken with 4 to 8 weeks of cold storage (Bonner and Vozzo 1987). Germination during storage is common among acorns of both sections. This does not usually reduce seedling vigor so long as radicle extension is not too advanced, but progress of mechanical sowing activities is hindered when lengthy radicles obstruct sowing machinery. Lastly, overnight soaking in cool water is an important final preparation for sowing—it replaces moisture loss during storage ensuring acorns are fully hydrated for the field environment.

5 Plantation establishment

5.1 Plantation design

As previously mentioned, the various bottomland oaks show a stratified distribution among sites common to floodplains of the southern US (Table 1). Well-designed plantations are intended to target the natural occurrence of species characteristic of the floodplain sites represented at the restoration area. This usually includes other bottomland tree species occurring in association with bottomland oaks. In designing the plantation, the restoration manager would select the most site-appropriate species mixtures for the occurrence of site types and associated soils at the area. For example, if sites on the restoration area were sloughs, low flats, and ridges, the slough sites would receive overcup oak, low flats would receive Nuttall oak (*Q. texana* Buckley) and ridges would receive cherrybark oak (*Q. pagoda* Raf.), swamp chestnut oak (*Q. michauxii* Walter) and water oak (*Q. nigra* L.).

Sowing densities for regenerating bottomland oak stands are generally based on a targeted stem density weighted by the expected germination and early seedling survival for a given species and site. While germination and first-year survival for most bottomland oaks on their respective sites can exceed well over 50%, second year mortality is usually high, and the manager can expect about 15 to 20% survival and establishment after year 2 (Table 4). Nuttall oak is a notable exception, often averaging about 30% germination and seedling survival though year 2. Expected survival and establishment will be lower on unusually harsh sites, for example, those subject to atypical flooding in the growing season or those extremely degraded from past cultural practices.

Table 4. Acorn sowing characteristics for 10 oak species common to bottomlands of the southern US.

Species	Nut length[1] (mm)	Number per kg[2]	Sowing depth[3] (cm)	Sowing season[4] (month)	Expected year 2 establishment[5] (%)
			Section Quercus		
Overcup oak (*Q. lyrata* Walter)	12–25	285–340	5–10	October–June	10–20
Swamp chestnut oak (*Q. michauxii* Walter)	19–38	75–430	5–10	October–March	10–20
White oak (*Q. alba* L.)	19–25	155–465	5–10	October–March	10–20
			Section Lobatae		
Cherrybark oak (*Q. pagoda* Raf.)	10–15	925–1640	3–7.5	November–March	15–25
Nuttall oak (*Q. texana* Buckley)	19–31	125–315	5–10	November–June	25–35
Pin oak (*Q. palustris* Münchh.)	9–13	705–1190	3–7.5	November–June	15–25
Water oak (*Q. nigra* L.)	8–16	510–1545	3–7.5	November–April	15–25
Willow oak (*Q. phellos* L.)	10–15	600–1530	3–7.5	November–April	15–25
Shumard oak (*Q. shumardii* Buckley)	19–25	170–280	5–10	November–March	15–25
Swamp laurel oak (*Q. laurifolia* Michaux)	10–12	860–1520	3–7.5	November–June	15–25

[1] Information from Vines (1960) adapted to include unpublished observations of the authors.
[2] Information from Bonner (2008) adapted to include unpublished observations of the authors.
[3] The range in recommended sowing depth is based on seed size, Johnson (1981), Johnson (1983), Gardiner et al. (2004), and unpublished observations of the authors.
[4] Sowing for all bottomland oaks will usually occur between December and March but all species can be sown as early as November to avoid storing seed if soil on the area is sufficiently moist. If the restoration area is inundated by floodwater, sowing can be delayed into late spring or early summer depending on species and the floodplain site it naturally occupies, i.e. sowing date can be delayed greatest for species of lowest sites.
[5] Based on information in Johnson (1983), Miwa et al. (1993), Gardiner et al. (2004), and unpublished observations of the authors.

Afforestation of former agricultural land largely results in single cohort stands, i.e., seeding for a stand occurs at one time. On sites where establishment of multiple oak species is appropriate, acorns are mixed prior to sowing in proportion to the desired establishment density of each species. It should be noted that practices for seeding bottomland tree species other than the oaks are not well developed; exceptions include for the species sweet pecan (*Carya illinoensis* (Wangenh.) K.Koch) and common persimmon (*Diospyros virginiana* L.). This lack of applied knowledge often leads the restoration manager to rely on planting seedlings rather than seeding to restore tree cover because achieving the high species diversity characteristic of natural stands is usually an objective when restoring bottomland hardwood forests.

Interplanting a fast-growing pioneer species, eastern cottonwood, with bottomland oaks is an alternative plantation design that has gained use in the LMAV over the last two decades (Gardiner et al. 2004). Those using this approach on restoration sites typically interplant established eastern cottonwood with bottomland oak bareroot seedlings. However, seeding oaks could readily replace planting bareroot seedlings as a lower-cost approach, and this approach has been successfully demonstrated in Europe where oaks and beech (*Fagus sylvatica* L.) have been sown under established poplar (*Populus* spp. L.) cultivars.

5.2 Sowing practices

The acorn sowing season in the southern US is usually December through early March. Nevertheless, sowing species of the section Quercus can be initiated much earlier—storage can be avoided, and acorns sown as soon as they are collected if soil moisture availability on the restoration area is high. Seeding by hand and tractor-drawn seeding machines have demonstrated equal success in sowing acorns of bottomland oaks. Regardless of method, the targeted sowing depth ranges between 3 and 10 cm. Relatively small acorns are usually sown on the shallow end of the depth range and relatively large acorns are sown towards the deeper end (Table 4). Field crews sowing bottomland oak acorns by hand often use a 2 to 2.5 cm diameter rod sharpened to a blunt cone on one end for forming the seeding hole. An acorn is dropped into the hole and the crew member covers it by stomping around the hole with a boot heel. Despite the fact that it is labor intensive, hand sowing is advantageous on bottomland sites too wet to be trafficked by heavy machinery. Seeding with machines has traditionally been conducted with row crop seed planters modified to dispense seed as large as an acorn. When conditions are favorable in the restoration area, machine sowing can be quite fast, especially if multiple seed planters are attached to an implement tool bar to allow for sowing several rows with each pass of the tractor.

Practices to protect sown acorns from rodent depredation are typically not used on restoration sites in the southern US. Previously stated recommendations for site preparation and early season vegetation control are usually sufficient for temporarily reducing rodent habitat and minimizing seed losses due to depredation. An exception to this generality is where the restoration area borders existing forests or fallow fields. In such situations, the restoration manager will want to plan for protecting seed sown adjacent to the existing forest or fallow field edge, e.g., cultivating soil to temporarily reduce vegetative cover and animal movement between the restoration area and adjacent habitat.

6 Post-sowing practices and maintenance

Few post-sowing practices are used to improve establishment and early growth or protect bottomland oak plantations in the southern US. This is largely because plantation establishment and early maintenance are usually conducted as low intensity operations to minimize costs. However, competition control that targets herbaceous broadleaves and grasses during the first growing season can be beneficial to early growth and improve establishment of the recently sown plantation. Applications of a broad-spectrum tank mix of herbicides labeled for use in oak plantations can be used to reduce aggressive weeds that are ever present on former agricultural land, and such practices can also retard development of rodent habitat while seedlings are most vulnerable to damage (see previous discussion).

The restoration manager should consider a few practices to protect the young plantation from external threats, especially where the restoration area is adjacent to current agriculture. Conventional agricultural practices in the southern US typically include aerial application of broadleaf herbicides. It is prudent for the restoration manager to communicate details of the forest restoration project with adjacent farmers and local aerial applicators to ensure necessary precautions are taken to prevent herbicide drift onto the restoration area. Also, it is common practice in the southern US to burn agricultural fields in the fall following the harvest of crops. Former agricultural fields that have been afforested are ideal for supporting dense growth of grasses and herbaceous vegetation that is readily flammable in the dry months of fall. Thus, protecting plantations from fire during this season, by maintaining appropriately located firebreaks, can prevent damage or loss of young bottomland oak stands.

7 Successful seeding

7.1 Defining success

Because the financial driver of forest restoration in bottomlands has historically been the singular impetus of removing land from agricultural production, success with seeding of bottomland oaks on former agricultural fields has simply been defined in respect to stand establishment and early growth. In practice, managers usually schedule inventory of seedling establishment and growth late in the third growing season after sowing. Small circular plots or linear row plots established systematically across the restoration area and stratified by soil series or site type are conventionally used to sample the restoration area. Circular plots are used if the manager samples seeded oaks plus other volunteer reproduction, while row plots that straddle sown rows are used if the manager is only concerned with sampling seeded oaks. A minimum threshold stand density for success is often arbitrary and may or may not include density of volunteer reproduction. Likewise, a minimum threshold for seedling or sapling growth is also arbitrary but should factor expected site productivity and status of competing vegetation. On average, year 3 densities of about 500 to 550 oak seedlings per ha, of sufficient vigor to out-grow adjacent competing vegetation, and well distributed across the area will be sufficient to mark success for most bottomland oak seeding objectives. Threshold densities for bottomland oak establishment would be reduced where volunteer reproduction of other native tree species, e.g., sweetgum, green ash, eastern cottonwood, common persimmon, and red maple (*Acer rubrum* L.), has established (Figure 7).

Figure 7. Stand of Nuttall oak (*Q. texana* Buckley) showing establishment and development 10 years after seeding the restoration site in Sharkey County, Mississippi USA. Oaks are the prominent vegetation in the image but other tree and shrub species that seed in naturally can be seen in the foreground (Photo credits: Emile Gardiner).

Over time, landowners and restoration program managers have begun to assess other metrics of restoration success, particularly where restoration is applied for specific environmental technologies or ecosystem services. For example, afforestation is a key nature-based tool for mitigating CO_2 emissions, so many bottomland forest restoration projects are now motivated by carbon sequestration and storage (Shoch et al. 2009). In these situations, managers may assess the short-term success of stand establishment but also assess the success of carbon sequestration and storage through verification of carbon stocks development over decades.

7.2 Factors that limit success and impose risks

Numerous factors have been associated with poor success of seeding bottomland oaks on former agricultural land, all which challenge attainment of sufficient seedling stocking on the restoration area. Poor seedling stocking often stems from sowing inferior quality seed which includes seed that lacks viability and seed originating from an inappropriate genetic source. Viability may be compromised prior to collection if microsite conditions around the parent tree are deleterious to the shed acorns, e.g., insufficient moisture in the litter layer. Seed quality, or acorn viability, can also be compromised through poor storage and handling practices. During storage, desiccation, rotting, or excessive premature germination will decrease viability and vigor when acorns are stored too long, too dry, too wet, or too warm. Allowing acorns to dry excessively or overheat during transport to the field or in the field prior to sowing will also reduce viability. Seed from an inappropriate genetic source includes acorns sourced too distant from the restoration site or those sourced from upland ecotypes of bottomland oak species. Acorns collected too distant from the restoration site may potentially express a germination or seedling phenology that jeopardizes survival of the sprouting seed, e.g., increased risk of frost damage. Seedlings produced from acorns collected from upland ecotypes of bottomland oaks, especially cherrybark oak, water oak, and white oak (*Q. alba* L.), may lack an inherent ability to tolerate soil flooding in bottomlands. Unfortunately, the hazards of sourcing inappropriate seed may not be revealed through establishment success or early stand performance but through other chronic issues like poor root architecture that renders trees susceptible to wind throw, or canopy dieback that decreases tree vigor and increases susceptibility to pests and disease later in the life of the stand.

Experience indicates that quality seed will typically not mitigate the risks of a poor sowing job. Sowing quality seed off-site, which can result from misguided species assignments or erroneous implementation of the seeding plan, will limit seedling establishment and early growth due to poor adaptability of the seed to the site on which it was sown. Likewise, sowing acorns too deep or too shallow reduces the probability for high establishment success, as does sowing a site that has not received adequate site preparation or post-sowing vegetation control. Managers often report spatially heterogenous or "patchy" stocking of bottomland oaks on seeded sites—this establishment result may not be due to a single cause on all sites but likely stems from a combination of multiple issues mentioned above.

Factors imparting risks that are less predictable and difficult to moderate are associated with local weather patterns during the establishment year. These include heavy rainfall that inundates the restoration area or waterlogs soil at a vulnerable time for newly sprouted seedlings, and a lengthy period of droughty conditions during the establishment year. Such weather or climatic events that produce extremes on each end of the hydrologic gradient will increase seedling mortality and can potentially lead to complete failure in stand establishment. Such extreme events could increase in frequency under future climatic conditions (Cai et al. 2014).

7.3 Elements that contribute to success

Success with seeding bottomland oaks begins with sound formulation of the restoration plan (Figure 8). Because alluvial bottomlands inherently show great spatial heterogeneity of site and soil conditions, the plan should be founded on thorough evaluation and detailed mapping of the topographic features, soil series, soil degradation, flooding frequency, water holding and drainage structures, and vegetation occurring on the restoration area. Compiling, organizing, and mapping such comprehensive information on the area enables the manager to make appropriate species assignments, prescribe site preparation treatments, establish sowing densities, anticipate seed depredation and herbivory, and prepare for other situations that might arise from degraded conditions of the site.

Committed implementation of the restoration plan is equally important to the success of bottomland oak seeding as formulating the plan. Securing quality seed, adequate preparation of the area for sowing, use of sound seed handling and sowing procedures, effective application of post-sowing treatments and practices, and timely monitoring of stand establishment and environmental conditions at the restoration area all contribute to purposeful implementation of the restoration plan. The likelihood of achieving committed implementation of the restoration plan is high when it is entrusted to a competent and dedicated restoration manager.

Figure 8. Closed-canopy stand of Nuttall oak (*Q. texana* Buckley) showing development 29 years after seeding the restoration site in Sharkey County, Mississippi USA. Notice the significant component of vines that provide natural structure to the stand. This is the same stand pictured in Figure 7 nineteen years later (Photo credits: Emile Gardiner).

In addition to sound formulation and committed implementation of the restoration plan, certain conditions relative to the restoration area can also contribute to success in restoring bottomland oak forests through seeding. Seeding success is often best on restoration areas where there is a high probability that light seeded tree species will contribute volunteer reproduction. This is because bottomland oak stands tend to develop a healthy and resilient structure when the oaks comprise a fraction (≤ 50%) of the overstory composition. On restoration areas seeded exclusively with bottomland oaks, species rich overstories tend to develop if the area is relatively small, adjacent to natural forest, and has received site preparation that conditions the seedbed for capture and germination of light seeded species. Conversely, large restoration areas distant from seed sources for other tree species may be captured by herbaceous species and vines.

Similarly, assigning more than one oak species and section to sites or soils that are naturally suitable for multiple oaks is often important to success. Sowing multiple oaks on a site could buffer against risks associated with a single species, e.g., poor quality seed or inappropriate seed source that impacts germination and establishment. In this respect, seeding species of both bottomland oak sections (Lobatae and Quercus) adds diversity in factors like germination dynamics, rate of seedling growth, and shade tolerance which should ultimately benefit stand composition.

8 Conclusion

In summary, the rich forests native to river bottoms of the southern US have experienced persistent and wide-scale loss and degradation since the 1700s, due mostly to deforestation for agriculture. The most recent decades, however, have brought efficiencies in agriculture and a growing awareness of the environmental and ecological values of these systems, and this has prompted considerable forest restoration. Development of techniques and practices to seed bottomland oaks coalesced in the early 1980s prior to broad implementation of afforestation to restore bottomland oak forests across the region. While the early seeding techniques and practices have been refined for large-scale application to degraded sites, the biological and ecological foundations of seeding bottomland oaks have endured over time. These have given rise to several silvicultural principles for seeding bottomland oaks including matching oak species to appropriate sites, procuring quality seed, practicing sound seed handling and sowing, sowing multi-species mixtures where possible, and monitoring conditions and stand development across the restoration area. Adherence to these principles through development and implementation of the restoration plan reduces risks and bolsters success of seeding to restore bottomland oak forests of the southern US.

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10 References

Allen JA (1990) Establishment of bottomland oak plantations on the Yazoo National Wildlife Refuge Complex. South J Appl For 14:206–210. https://doi.org/10.1093/sjaf/14.4.206

Baker JB, Broadfoot WM (1979) A practical field method of site evaluation for commercially important southern hardwoods. USDA Forest Service General Technical Report SO-26, New Orleans, LA, USA.

Battaglia LL, Minchin PR, Pritchett DW (2002) Sixteen years of old-field succession and reestablishment of a bottomland hardwood forest in the Lower Mississippi Alluvial Valley. Wetlands 22:1–17. https://doi.org/10.1672/0277-5212(2002)022[0001:SYOOFS]2.0.CO;2

Bonner FT (2008) Fagaceae – beech family, *Quercus* L. oak. In: Bonner FT, Karrfalt, RP (eds) and Nisley RG (ed coord), The woody plant seed manual. USDA Forest Service Agriculture Handbook 727, Washington DC, USA, pp 928–938.

Bonner FT, Vozzo JA (1987) Seed biology and technology of *Quercus*. USDA Forest Service General Technical Report SO-66. New Orleans, LA, USA.

Burns RM, Honkala BH (tech coords) (1990) Silvics of North America Volume 2. Hardwoods. USDA Forest Service Agriculture Handbook 654, Washington DC, USA.

Cai W, Borlace S, Lengaigne M, Van Rensch P, Collins M, Vecchi G, Timmermann A, Santoso A, McPhaden MJ, Wu L, England MH, Wang G, Guilyardi E, Jin FF (2014) Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change 4:111–116. https://doi.org/10.1038/nclimate2100

Cannon JB, Peterson CJ, Godfrey CM, Whelan AW (2023) Hurricane wind regimes for forests of North America. Proc Nat Acad Sci United States America 120(42):e2309076120(1–8). https://doi.org/10.1073/pnas.2309076120

Cunningham K, Taylor E, Barber B, Holley G, Blazier M (2019) Forestry herbicide prescriptions – Western Gulf Region. University of Arkansas, Division of Agriculture Research and Extension, MP553.

DeSteven D, Schweitzer CJ, Hughes SC, Stanturf JA (2015) Afforesting agricultural lands in the Mississippi Alluvial Valley (USA): effects of silvicultural methods on understory plant diversity. In: Holley AG, Connor, KF, Haywood JD (eds) Proceedings of the 17th Biennial Southern Silvicultural Research Conference. USDA Forest Service, Southern Research Station, e-General Technical Report SRS-203. Asheville, NC, USA, pp 29–35.

Gardiner ES (2014) Outlook for Mississippi Alluvial Valley forests: a subregional report from the Southern Forest Futures Project. USDA Forest Service, Southern Research Station, General Technical Report SRS-201. Asheville, NC, USA. https://doi.org/10.2737/SRS-GTR-201

Gardiner ES, Hodges JD, Fristoe TC (2004) Flood plain topography affects establishment success of direct-seeded bottomland oaks. In: Connor KF (ed) Proceedings of the 12th Biennial Southern Silvicultural Research Conference. USDA Forest Service, Southern Research Station, General Technical Report SRS-71. Asheville, NC, USA, pp 581–585.

Gardiner ES, Stanturf JA, Schweitzer CJ (2004) An afforestation system for restoring bottomland hardwood forests: biomass accumulation of Nuttall oak seedlings interplanted beneath eastern cottonwood. Rest Ecol 12:525–532. https://doi.org/10.1111/j.1061-2971.2004.00396.x

Groninger JW, Aust WM, Miwa M, Stanturf JA (2000) Growth predictions for tree species planted on marginal soybean lands in the Lower Mississippi Valley. J Soil Water Conserv 55:91–95. https://doi.org/10.1080/00224561.2000.12457314

Hodges JD (1995) The southern bottomland hardwood region and brown loam bluffs subregion. In: Barrett JW (ed) Regional silviculture of the United States. John Wiley & Sons, Inc, New York, USA, pp 227–269.

Hodges JD (1997) Development and ecology of bottomland hardwood sites. For Ecol Manag 90:117–125. https://doi.org/10.1016/S0378-1127(96)03906-0

Hunter RG, Faulkner SP, Gibson KA (2008) The importance of hydrology in restoration of bottomland hardwood wetland functions. Wetlands 28:605–615. https://doi.org/10.1672/07-139.1

Johnson RL (1981) Oak seeding—it can work. South J Appl For 5:28–33. https://doi.org/10.1093/sjaf/5.1.28

Johnson RL (1983) Nuttall oak direct seedings still successful after 11 years. USDA Forest Service, Southern Forest Experiment Station, Research Note SO-301, New Orleans, LA, USA. https://doi.org/10.2737/SO-RN-301

Johnson RL, Krinard RM (1985) Oak seeding on an adverse field site. USDA Forest Service, Southern Forest Experiment Station, Research Note SO-319, New Orleans, LA, USA. https://doi.org/10.2737/SO-RN-319

Kennedy HE, Nowacki GJ (1997) An old-growth definition for seasonally wet oak-hardwood woodlands. USDA Forest Service, Southern Research Station, General Technical Report SRS-8, Asheville, NC, USA. https://doi.org/10.2737/SRS-GTR-8

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. For Ecol Manag 448:474–489. https://doi.org/10.1016/j.foreco.2019.06.032

MacDonald PO, Frayer WE, Clauser JK (1979) Documentation, chronology, and future projections of bottomland hardwood habitat loss in the Lower Mississippi Alluvial Plain: Basic report. Vol. 1, US Fish and Wildlife Service, Washington, DC, USA.

McNulty S, Myers JM, Caldwell P, Sun G (2013) Chapter 3 – Climate change summary. In: Wear DN, Greis, JG (eds) The Southern Forest Futures Project: technical report. USDA Forest Service, Southern Research Station, General Technical Report SRS-178, Asheville, NC, USA, pp 27–43. https://doi.org/10.2737/SRS-GTR-178

Meadows JS, Nowacki GJ (1996) An old-growth definition for eastern riverfront forests. USDA Forest Service, Southern Research Station, General Technical Report SRS-4, Asheville, NC, USA https://doi.org/10.2737/SRS-GTR-4

Miwa M, Schoenholtz SH, Hodges JD, Kennedy HE Jr (1993) First-year results of bottomland oak reestablishment in alluvial soils of the Lower Mississippi Valley. In: Brissette JC (ed) Proceedings of the Seventh Biennial Southern Silvicultural Research Conference. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO-93, New Orleans, LA, USA, pp 73–79.

Muller RA, Grymes, III JM (1998) Regional climates. In: Messina MG, Conner WH (eds), Southern forested wetlands ecology and management. Lewis Publishers, Boca Raton, FL, USA, pp 87–101.

NOAA (2023) National Oceanic and Atmospheric Administration, National Centers for Environmental Information, 1991–2020 Normals. http://www.ncdc.noaa.gov/cdo-web/datatools/normals. (last accessed 15 May 2024).

NRCS (2020) Soil Survey Staff, USDA, Natural Resources Conservation Service. Web Soil Survey. http://websoilsurvey.sc.egov.usda.gov/. (last accessed 15 May 2024).

Oliver CD, Burkhardt EC, Skojac DA (2005) The increasing scarcity of red oaks in Mississippi River floodplain forests: Influence of the residual overstory. For Ecol Manag 210:393–414. https://doi.org/10.1016/j.foreco.2005.02.036

Ouyang Y, Jin W, Grace JM, Obalum SE, Zipperer WC, Huang X (2019) Estimating impact of forest land on groundwater recharge in a humid subtropical watershed of the Lower Mississippi River Alluvial Valley. J Hydrol: Regional Studies 26:100631(1–13). https://doi.org/10.1016/j.ejrh.2019.100631

Putnam JA, Bull H (1932) The trees of the bottomlands of the Mississippi River Delta region: their distribution, occurrence by site and cover type, utilization in the Delta, and the distinguishing characteristics of the principal and most common species and groups of species. USDA Forest Service Southern Forest Experiment Station, New Orleans, LA, USA.

Shoch DT, Kaster G, Hohl A, Souter R (2009) Carbon storage of bottomland hardwood afforestation in the Lower Mississippi Valley, USA. Wetlands 29(2):535–542. https://doi.org/10.1672/08-110.1

Stanturf JA, Schoenholtz SH (1998) Soils and landforms. In: Messina MG, Conner WH (eds) Southern forested wetlands ecology and management. CRC Press Lewis Publishers, Boca Raton, FL, USA, pp 123–147. https://doi.org/10.4324/9780429342653-6

Stanturf JA, Gardiner ES, Hamel PB, Devall MS, Leininger TD, Warren ME Jr (2000) Restoring bottomland hardwood ecosystems in the Lower Mississippi Alluvial Valley. J For 98(8):10–16. https://doi.org/10.1093/jof/98.8.10

Stanturf JA, Conner WH, Gardiner ES, Schweitzer CJ, Ezell AW (2004) Recognizing and overcoming difficult site conditions for afforestation of bottomland hardwoods. Ecol Restor 22:183–193. https://doi.org/10.3368/er.22.3.183

Stanturf JA, Goodrick SL, Outcalt KW (2007) Disturbance and coastal forests: A strategic approach to forest management in hurricane impact zones. For Ecol Manag 250:119–135. https://doi.org/10.1016/j.foreco.2007.03.015

Sternitzke HS (1976) Impact of changing land use on Delta hardwood forests. J For 74(1):25–27. https://doi.org/10.1093/jof/74.1.25

Strickland MS, Callaham MA Jr, Gardiner ES, Stanturf JA, Leff JW, Fierer N, Bradford MA (2017) Response of soil microbial community composition and function to a bottomland forest restoration intensity gradient. Appl Soil Ecol 119:317–326. https://doi.org/10.1016/j.apsoil.2017.07.008

Vines RA (1960) Trees, shrubs and woody vines of the southwest. University of Texas Press, Austin, TX, USA.

Seeding of oak in southern Sweden

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Abstract

Sweden is known for its coniferous forests, but two oak species occur in the south, *Quercus robur* and *Q. petraea*, in pure stands or mixed with other species. Oak forests have declined due to land use changes, industrial forestry favoring conifers, and browsing by wild ungulates. Oak grows best on deep, fertile soils but can survive on a range of sites, supporting high biodiversity, and have cultural, aesthetic, and recreational value. The temperate climate is expected to change, and the increased temperature and rainfall potentially will favor oak over other species. Historically, high sowing rates and low-cost labor contributed to successful oak establishment; planting has since become the main method. Interest in seeding is returning, but predation and germination risks make it less certain than planting. Site preparation and high seeding density can help mitigate losses where heavy acorn predation by rodents is expected. Competition from other vegetation requires intensive mechanical site preparation and periodic cleaning operations. Seeding is more successful on abandoned farmland with less rodent habitat and where agricultural practices can be used for site preparation and maintenance. Expensive fencing is required for protection from browsing, especially in the first 10 years. Restoration success requires regular assessment and management, with lower oak seedling densities acceptable if other species are present. Lack of experience among managers is a barrier; more information and communication about successful practices are needed.

Keywords

Quercus, direct seeding, seed predation, ungulate browsing, afforestation, manager inexperience

Contents

1 The forest

Forests in Sweden are mostly coniferous forests of the boreal region. The two main tree species are Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.). However, there are two oak (*Quercus* spp. L.) species from the section Quercus found in southern Sweden, pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.), and they overlap considerably in range, forest types, and ecological characteristics (Gömöry et al. 2001). Oak-dominated forests in the region have gradually declined over recent millennia due to several factors such as changed land use, introduction of industrial forestry that has promoted conifers over broadleaves, and more recently, over-browsing by wildlife (Petersson et al. 2019). Today, oaks are distributed south of Limes Norrlandicus, the northern limit of the temperate forest zone in Sweden, i.e., ca. 100 km north of the capital city Stockholm (Sjörs 1999) (Figure 1). Oak stands are mainly found on fertile sites with deep soils, often in the transition between farmland and coniferous forest, but also on nutrient-poor sites in coastal areas (Löf et al. 2016).

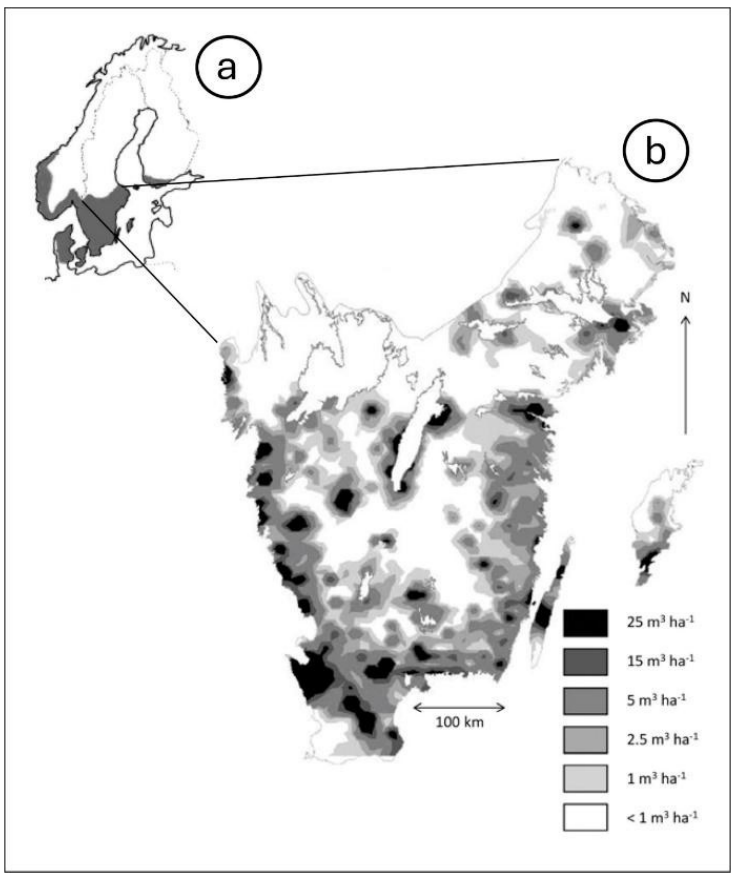

Figure 1. Distribution of standing volume of oak in southern Sweden south of 'Limes Norrlandicus,' the northern limit of the temperate forest zone. The Nordic countries with distribution of oaks (grey) (a), and southern Sweden with standing volumes of oaks (b). The data is derived from the Swedish University of Agricultural Sciences and the Swedish National Forest Inventory (SLU-SNFI) during the years 1993–1997.

In the southern region, oak is a minor part of the total standing volume, i.e., 4%, which is dominated by Norway spruce, Scots pine, and birch (*Betula* spp. L.) (SLU 2020).

The oaks occur in pure stands for timber production but also in mixtures with other tree species such as Norway spruce, Scots pine, and birch (Drössler et al. 2012). Many of these pure oak or oak-rich mixed forests derive from past land uses such as wood pastures, coppice, or abandoned agricultural lands. Small private forest owners own most oak-dominated forests, and although the owners focus on timber production, oak wood production often plays a minor role in the economy of these forest owners.

The climate of southern Sweden is temperate, corresponding to Central European weather conditions. There are four distinct seasons and mild temperatures throughout the year. Extreme southern Sweden corresponds to Köppen Cfb oceanic, while the more northerly portion of the region corresponds to Dfb warm-summer continental climate. Mean annual precipitation decreases from about 1000 mm in the west to 600 mm in the east, and the mean temperature ranges from −3 °C in January to 16 °C in July (reference time span 1961–1990) (SMHI 2025). The climate that favors oak is warm springs and summers with relatively high annual precipitation. Cold winters may kill acorns that are not well protected in the forest floor, and late spring frost may damage flowers and young seedlings, thus limiting the regeneration process (Löf et al. 2019). For the region, temperatures are expected to increase by 2–6 °C by the end of this century and the warming will be more pronounced in winter than in summer. It is thought that total annual rainfall will increase over southern Sweden by about 10%, but simulations suggest that summer drought with high temperatures may become common in the eastern parts. Additionally, the weather is expected to become more extreme, with heavier rainfall events, longer dry periods, and more frequent gales with high wind speed (Aldea et al. 2024). Generally, the projected shifts in climate are considered to favor oak relative to other tree species (Dyderski et al. 2017).

Oak stands are found on a wide range of soils and trees survive well on both relatively moist and dry sites (Carbonnier 1975). The best growth of oak is found on deep soils with a clay content, i.e., on land most often used for agriculture. Here, pure oak stands can produce up to 6 m^3 ha^{-1} yr^{-1}. At the end of the rotation period, such stands may have a basal area of about 20 m^2 ha^{-1} and an average tree height of 30 m. On poorer and drier soils, growth and tree density is much lower, perhaps around 1 m^3 ha^{-1} yr^{-1} volume with basal areas of ca. 10 m^2 ha^{-1}. Such stands are often found along the coasts of southern Sweden (Figure 1).

Oak trees and forests are associated with high biodiversity and a range of aesthetic, symbolic, religious, recreational, and historical values, and are generally favored by the public. Oak-dominated forests support high biodiversity (Mölder et al. 2019). This is because they are generally more open than other forests, are allowed to age, and the trees themselves produce important micro-habitats. For example, bark that is sun-exposed is important for a wide range of insects, and older oaks have coarse bark, branches in various stages of decay, retain a lot of dead wood, and may have many cavities (Ranius et al. 2008, Paltto et al. 2011). Policies relating to oak forests have primarily concentrated on protecting the most biodiversity rich sites and protecting remaining stands from conversion to other land uses, primarily conifer-dominated forestry (Löf et al. 2016). To compensate forest owners for the associated silvicultural costs of managing oak forests, regeneration and early stand management of oak stands are subsidized.

Nowadays there is much interest in using oak forests and mixed broadleaved forests as an adaptation strategy to climate change. Although the volume production of oak forests is lower compared to coniferous forests, it is considered to be more ecologically and economically stable. Oak forests rarely blow down during gales, the species are considered to be more drought-tolerant relative to many other tree species, and they are tolerant to various insects (Bolte et al. 2009). In addition, at the end of the rotation period, the value of oak timber can be very high. Policies to promote oak forests are developed by European Union and national authorities, and many forest owners are interested. However, there is little information, guidelines, or resources available for managers who want to restore oak forests.

2 History of southern Swedish forests and forest degradation

Land use history in Europe has led to the fact that only ca. 0.2% of the European temperate broadleaved forests remain in a near-natural condition (Hannah et al. 1995). As such, the temperate broadleaved forest represents one of the most degraded ecosystems in the world. More such forests remain as managed forests and in southern Sweden approximately 6% of the total standing volume consists of temperate broadleaved tree species with oaks as the dominant species (Anonymous 2024). Temperate broadleaved forests covered much larger areas historically than they do today (Björse and Bradshaw 1998; Lindbladh et al. 2014). Scandinavia was covered with ice until about 10,000 years ago, and about 6,000 years ago temperate deciduous forest dominated the region. Thereafter, the share of temperate broadleaved forest declined due to a combination of factors such as a less favorable climate, colonization by other tree species, and cultivation of the best soils. Over the last 200–300 years, temperate broadleaved forests were overexploited for timber, grazing, and firewood, and much land was cleared for farming (Spiecker et al. 2004). At the same time, industrialization created a need for more timber, which promoted reforestation and afforestation with faster growing conifers such as Norway spruce and Scots pine. During the last 80 years or so, Norway spruce has been the preferred species of industrial forestry because of its rapid growth, its easy establishment and management, and its unpalatability to browsing animals (Lodin et al. 2017). Therefore, forests in the region are dominated by these two conifer tree species, and forest industry is heavily dependent on this timber resource. In this forest landscape, dominated by conifer plantations and agricultural fields, oak-dominated forests occur as small fragments, and most of these forests are managed for timber production.

3 Mitigating impacts for seeding

Browsing by wild ungulates (Family Cervidae), such as moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), are the biggest challenge to regenerating oak in southern Sweden. Ungulate populations have increased during the last 50 years due to changes in game management, changes in land use, and milder winters (Petersson et al. 2019). Expensive fences, costing up to 20 Euros m^{-1}, are needed to protect seedlings, drastically increasing the total cost for regeneration (Figure 2). Fencing to prevent wild ungulate browsing should be maintained during the first 10 years following establishment. Thereafter, oak seedlings most often have reached a browsing free height, and the fencing can be removed, which is also a cost. Most often, 2-meter-tall, metal-wire fencing is needed to protect regeneration areas from moose, but lower cost fences can be used if moose are not present at the site. Some research is ongoing to investigate low-cost alternatives to tall metal-wire fencing, for example, wooden fences, slash fences, or ecological solutions like establishment of thorny plants or use of repellents. However, clear results and direction for implementation are yet to develop.

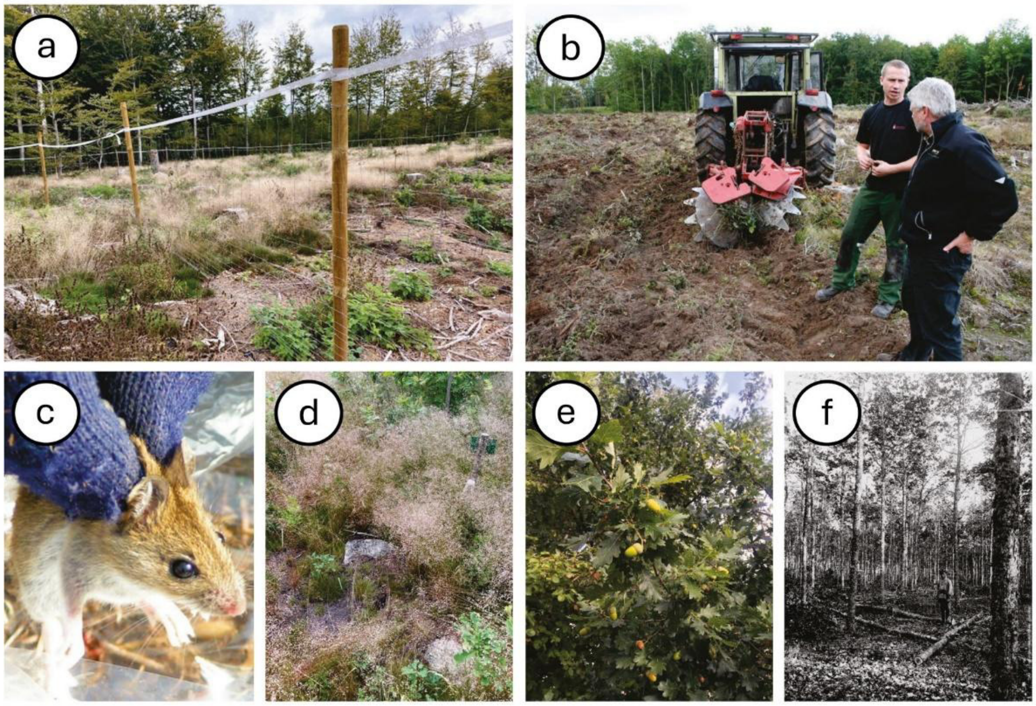

Figure 2. (a) Fenced area to regenerate oak through seeding in southern Sweden, (b) mechanical site preparation to prepare a site for seeding acorns, (c) a captured wood-mouse (*Apodemus sylvaticus*) within a seeded area, (d) newly established oak seedlings with competing vegetation, (e) *Q. robur* acorns still attached to tree in autumn, and (f) an oak forest (57 years old) established with seeding in 1867 in southern Sweden. (Photo credits: (a) Magnus Löf, (b) Palle Madsen, (c) Maria Birkedal, (d) Magnus Löf, (e) Gunnar Schotte, (f) Forest Library SLU, Umeå, Sweden.).

Because of their high energy and nutrient content, acorns are highly attractive to a wide range of animals including insects, birds, and mammals such as rodents (Order Rodentia) and wild boar (*Sus scrofa*) (Löf et al. 2019). Acorns shed to the forest floor are rapidly removed by animals and either consumed or hoarded for later consumption. Animals that cache or disperse acorns for later consumption may act as both predators of seed and facilitators of natural regeneration, because some acorns are dispersed to micro-sites suitable for seedling establishment. This is the case for many forest rodents including mice, rats (Family Muridae), and squirrels (Family Sciuridae). Rodents can remove acorns from forest restoration sites within weeks of sowing, even if acorns are buried (Villalobos et al. 2020) (Figure 2). Granivorous rodents use their sensitive olfactory sense to locate buried seeds. Rodents prefer sites with some tree cover or where other protection is available, e.g., stones, bushes, stumps, grasses, etc. It is therefore difficult to establish oak by seeding on forest land where rodent habitats are available. Several potential tools for protection from small mammals have been tested; these include seed and seedling tubes, mechanical site preparation, and repellants made from predator odors (Löf et al. 2019). None of these have so far been shown to work on a practical scale and it has proven very costly to protect individually sown seeds. However, when seeding larger clearcuts (> 1 ha) substantial amounts of acorns will escape predation, especially if little ground vegetation is present at the site (Villalobos et al. 2020). Thus, the size and proper site preparation of the regeneration area should be considered. In such cases, the local rodent population cannot remove all acorns if seeding density is sufficient—acorns that are not predated may produce a satisfactory number of seedlings to regenerate the area.

Seeding acorns works well on abandoned farmland where small rodent habitat is lacking. At such sites (abandoned farmland with no vegetation), the seeding operation can be performed with agricultural machines and equipment, herbicides are allowed for controlling competing vegetation, and therefore costs can be drastically reduced to approximately one-third of the costs of planting seedlings (Madsen and Löf 2005).

An additional challenge to newly established oak seedlings, on both forest and former farmland sites, is competition from other vegetation. Oaks are normally regenerated on fertile sites that support rapid colonization and growth of herbaceous and woody plants, and small seedlings can be outcompeted if this vegetation is not controlled (Löf et al. 2019). To control vegetation, intensive mechanical site preparation is needed on forest land, i.e. mounding or inverted mechanical site preparation. This will facilitate oak seedling establishment and growth during the first few years after sowing. Thereafter, cleaning operations are needed periodically during years 5 through 15 to release seedlings and saplings from competing vegetation. In southern Sweden, herbicides are not allowed to be used on forested land, so it is not an alternative during seeding operations at such sites.

4 Seed procurement and preparation

Acorns are collected on the ground manually by contractors in good seed years (mast years) (Löf et al. 2019). Sometimes nets can be laid out on the ground to simplify the process. There are a few nurseries in the region that buy and store acorns to cultivate oak seedlings. However, native seed or plant material is not always available. Seeds and seedlings are often purchased from dealers and nurseries in Denmark, Germany, Norway, Poland, and the Netherlands. Acorns are stored in high humidity and at temperatures around 0 °C. At the nurseries, seed quality is tested according to international standards, and acorns are treated with heat and fungicides to prevent fungal attacks. Some skilled foresters collect acorns themselves and store them over winter in jute bags that are lowered into streams of running water. This method was much more common in the past, when oak sowing was also more common.

5 Plant establishment

Acorn seeding is normally done in the spring, but sometimes acorns are sown in the fall. Fall sowing has the advantage that acorns do not need to be stored over winter, but the disadvantage that they are exposed to a longer period of predation by small rodents. On agricultural land, the seeding rate is about 70 kg ha^{-1} with a spacing of 2 m x 1 m (Löf M and Møller-Madsen 1997). The site should be harrowed before sowing to improve seedbed conditions for germination. After sowing, harrowing should be done again to cover the seed with soil. The site should then be treated with herbicides to minimize the establishment of competing vegetation.

On forest land, relatively large clearings (> 1 ha) can be sown successfully if intensive mechanical site preparation is used and sowing density is high (> 100 kg ha^{-1} acorns, spacing 1 m x 1 m) (Löf and Madsen 1998). In the 19th century, when oak seeding was more common, very high sowing densities were used (up to 10 acorns at each seeding spot) and poisons were used to protect the seed from small rodents (Carbonnier 1975). There are few successful examples of sowing acorns when a dense tree layer occupies the site, e.g., sowing under dense shelterwoods or in small gaps. In such locations, small rodents thrive and seek shelter in the surrounding vegetation. Thus, the acorns need to be protected for a few months until the young oak seedlings are established. Some research has been conducted to find cost-effective countermeasures, such as effective repellents against seed predation by small rodents (Villalobos et al. 2023). However, so far, no practical solution has been identified. Chemicals that counteract predation and simultaneously do not harm small rodents are very expensive, and formulations that sustain repellent properties over time in natural environments have yet to be developed.

6 Successful seeding

From the early 1800s until the 1930s, virtually all oak forests established in southern Sweden were seeded. The success was partly due to the fact that foresters and landowners used very high sowing rates. Practices associated with seeding operations (seed collection and sowing) were done with a low-paid labor force typical of that time. After the 1930s, seedling planting became the main tool for afforestation and reforestation as fast-growing conifers were in demand and dominated as planting material.

Nowadays, interest in oak seeding has returned. More broadleaved forests are needed to adapt forests in Sweden to the changing climate and to protect biodiversity (Bolte et al. 2009). We need to learn to establish oak stands through seeding again and develop the practice into an effective regeneration option. Some guidelines for this are described in this article.

Sowing is currently a more uncertain method than planting. This is mostly due to predation on sown acorns but there are also risks during seed germination. Too, acorns can freeze or dry out before they germinate. Any failures need to be detected in time. Assessment of restoration success needs to be done twice a year during the first two years after establishment. Once seedlings are established, management during the first ten years should focus on reducing competition with other vegetation. If there is too much competing vegetation already established on the site at time of regeneration, seeding should not be used. Planting large bare-root seedlings is a better option because they compete better with surrounding vegetation. Motor-manual pre-commercial thinning should be done at least two to three times during the first ten years. Afterwards, fencing can be removed.

A limitation to achieving a larger area of restored oak forest through sowing is the lack of experience and competence of forest managers with this practice. Today, only a few managers know how to implement seeding practices for oak establishment. Therefore, although sowing has great potential to be developed in the long term, planting will dominate in the near future. In general, there is a need for more information and communication about successful oak restoration with seeding. Most often, a seedling density of 2,000 to 10,000 oak seedlings ha^{-1} is considered a successful operation. However, when establishing oak regeneration, seedling densities do not need to be so high. Area between oaks may be occupied by other tree species that add value to the stand and can be harvested at a profit. At the end of the rotation period of the oak (100–150 years in southern Sweden), there are typically only about 50–70 oaks ha^{-1}. If intensive management of the young oaks or groups of young oaks can be implemented and the surrounding natural vegetation managed more intensively during the beginning of the rotation, cost-effective alternatives to planting can be developed.

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This paper may include research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All use of pesticides must be registered by appropriate agencies before they can be recommended.

CAUTION

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

8 References

Aldea J, Dahlgren J, Holmström E, Löf M (2024) Current and future drought vulnerability for three dominant boreal tree species. Glob Change Biol 30:e17079. https://doi.org/10.1111/gcb.17079

Anonymous (2009) Statistical yearbook of forestry. Official Statistics of Sweden, Swedish Forest Agency, Jönköping, Sweden.

Björse G, Bradshaw R (1998) 2000 years of forest dynamics in southern Sweden: suggestions for forest management. For Ecol Manag 104:15–26. https://doi.org/10.1016/S0378-1127(97)00162-X

Bolte A, Ammer C, Löf M, Madsen P, Nabuurs G-J, Schall P, Spathelf P, Rock J (2009) Adaptive forest management in Central Europe – climate change, strategies and integrative concept. Scand J For Res 24:473–482. https://doi.org/10.1080/02827580903418224

Carbonnier C (1975) Produktionen av kulturbestånd av ek i södra Sverige. Studia Forestalia Suecica 125:1–89.

Drössler L, Attocchi G, Jensen AM (2012) Occurrence and management of oak in southern Swedish forests. Forstarchiv 83:163–169. https://doi.org/10.4432/0300-4112-83-163

Dyderski MK, Paz S, Frelich LE, Jagodzinski AM (2017) How much does climate change threaten European forest tree species distribution? Glob Change Biol 24:1150–1163. https://doi.org/10.1111/gcb.13925

Gömöry D, Yakovlev I, Zhelev P, Jedináková J, Paule L (2001) Genetic differentiation of oak populations within the *Quercus robur/Quercus petraea* complex in Central and Eastern Europe. Heredity 86(5):557–563. https://doi.org/10.1046/j.1365-2540.2001.00874

Hannah L, Carr JL, Lankerani A (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. Biodivers Conserv 4:128–155. https://doi.org/10.1007/BF00137781

Lindbladh M, Axelsson A-L, Hultberg T, Brunet J, Felton A (2014) From broadleaves to spruce – the borealization of southern Sweden. Scand J For Res 29:686–696. https://doi.org/10.1080/02827581.2014.960893

Lodin I, Brukas V, Wallin I (2017) Spruce or not? Contextual and attitudinal drivers behind the choice of tree species in southern Sweden. For Policy Econ 83:191–198. https://doi.org/10.1016/j.forpol.2016.11.010

Löf M, Madsen P (1998) Ek- och boksådd på skogsmark – ett alternativ till plantering? Fakta Skog 15/1998. SLU publikationstjänst, Uppsala, Sweden.

Löf M, Brunet J, Filyushkina A, Lindbladh M, Skovsgaard J-P, Felton A (2016) Management of oak forests: Striking a balance between timber production, biodiversity and cultural services. Int J Biodivers Sci, Ecosyst Serv Manag 12:59–73. https://doi.org/10.1080/21513732.2015.1120780

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Tamm review: Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. For Ecol Manag 448:474–489. https://doi.org/10.1016/j.foreco.2019.06.032

Löf M, Møller-Madsen E (1997) Ekskog till lågpris! Skog & Forskning 2:46–50.

Madsen P, Löf M (2005) Reforestation in southern Scandinavia using direct seeding of oak (*Quercus robur* L.) Forestry 78:55–64. https://doi.org/10.1093/forestry/cpi005

Mölder A, Meyer P, Nagel R-V (2019) Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur, Q. petraea*) forests: An overview. For Ecol Manag 437:324–339. https://doi.org/10.1016/j.foreco.2019.01.006

Ranius T, Johansson P, Berg N, Niklasson M (2008) The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. J Veg Sci 19:653–662. https://doi.org/10.3170/2008-8-18433

Paltto H, Nordberg A, Nordén B, Snäll T (2011) Development of secondary woodland in oak wood pastures reduces the richness of rare epiphytic lichens. PLOS ONE 6(9):e24675. https://doi.org/10.1371/journal.pone.0024675

Petersson LK, Milberg P, Bergstedt J, Dahlgren J, Felton AM, Götmark F, Salk C, Löf M (2019) Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: six decades of landscape-scale evidence. For Ecol Manag 444:299–307. https://doi.org/10.1016/j.foreco.2019.04.037

Sjörs H (1999) The background: Geology, climate and zonation. In: Rydin H, Snoeijs P, Diekmann M (Eds.) Swedish Plant Geography. Acta Phytogeogr Suecica 84:5–14.

SLU (Swedish University of Agricultural Sciences) (2020) Skogsdata 2020: aktuella uppgifter om de svenska skogarna från Riksskogstaxeringen. Department of Forest Resource Management, Swedish University of Agricultural Sciences (SLU), Umeå, Sweden.

Spiecker H, Hansen J, Klimo E,Skovsgaard JP Sterba H, Teuffel K von (2004) Norway spruce conversion – options and consequences. European Forest Institute, Research Report 18. Brill Academic Publishers, Leiden, The Netherlands.

SMHI (2025) Swedish Meteorological and Hydrological Institute. Retrieved from https://www.smhi.se/data. Last accessed 4 October 2025.

Villalobos A, Schlyter F, Olsson G, Witzell J, Löf M (2020) Direct seeding for restoration of mixed oak forests: Influence of distance to forest edge, predator-derived repellent and acorn size on seed removal by granivorous rodents. For Ecol Manag 477:118484. https://doi.org/10.1016/j.foreco.2020.118484

Villalobos A, Schlyter F, Dekker T, Larsson Herrara S, Birgersson G, Löf M (2023) Predator odor can reduce acorn removal by granivorous rodents in mixed oak forest stands. For Ecol Manag 548:121411. https://doi.org/10.1016/j.foreco.2023.121411

Seeding to establish Ravni Srem oak forests, Nothern Serbia

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Abstract

Broadleaf species dominate Serbia's diverse forests including the Srem Forest District, where oak regeneration is focused on the Ravni Srem portion of the district. Pedunculate oak (*Quercus robur* L.) is the dominant species, making up about 50% of standing volume. The most important supporting species in mixed stands are narrow-leaved ash (*Fraxinus angustifolia* Vahl) and common hornbeam (*Carpinus betulus* L.). Seeding is used when acorn crops are poor or absent. In good mast years, acorns are incorporated into the soil or sown mechanically (about 450 kg ha^{-1}), 2 to 5 cm deep in rows 0.7 m apart with acorns spaced 15 to 20 cm in a row. Seeds are manually collected from registered stands and orchards, and subject to quality testing, thermotherapy, and fungicide treatment before storage. Herbicides and arboricides are used to control competition. Fencing protects seeds and seedlings from animals; rodenticides, fungicides, and insecticides are applied as required. Regeneration areas are limited to 56.25 ha, with seed trees left for shelter. Sowing is done in autumn–winter using machines, with acorns spaced in rows. Early competition is controlled by herbicides. Mechanical weeding and fencing continue during the sapling phase. Fire lanes are established and maintained for up to 15 years. Success is measured by seedling establishment and survival after the first growing season. Impacts of invasive plants and animal damage are mitigated by site management and maintaining fencing. Failure is mainly due to unfavorable climatic factors. The moderate-continental climate is expected to experience increased temperature and precipitation by 2040.

Keywords

Quercus robur; Seed treatments; Thermotherapy; Arboricides; Wildlife damage; Rodenticide

Contents

1 The forest

The Republic of Serbia has a large biome diversity from north to south—steppe, broad deciduous forests, boreal forests, and high mountain tundra (Republic of Serbia 2010). Forests in Serba cover 2.8 million ha (36.8% of the total area of the country), of which 91% are semi-natural forests and 6.5% are planted forests (NFI 2023). Broadleaf species are dominant with 45% of all stands being primarily single species and 42% being mixed broadleaf stands; about 7% are pure conifer stands and the remaining 6% are mixed conifer and broadleaf or mixed conifer stands (NFI 2023). Of the 49 tree species recorded in Serbia by the National Forest Inventory (NFI), 40 are broadleaf species and 9 are conifer species, with European beech (*Fagus sylvatica* L.) being the most dominant species, followed by Turkey oak (*Quercus cerris* L.), sessile oak (*Q. petraea* (Matt.) Liebl.), and Hungarian oak (*Q. frainetto* Ten.) (Banković et al. 2009). Within the Northern Forest area, the Srem Forest District extends between 44° 37' 53'' and 45° 11' 37'' N latitude, and 18° 59' 45'' and 20º 21' 30'' E longitude (Figure 1). It is situated in the northwestern part of Serbia where it covers an area of 42,319 ha and is framed by Fruška gora Mountain in the north, the Sava River in the south, the Danube River in the east, and the Republic of Croatia in the west.

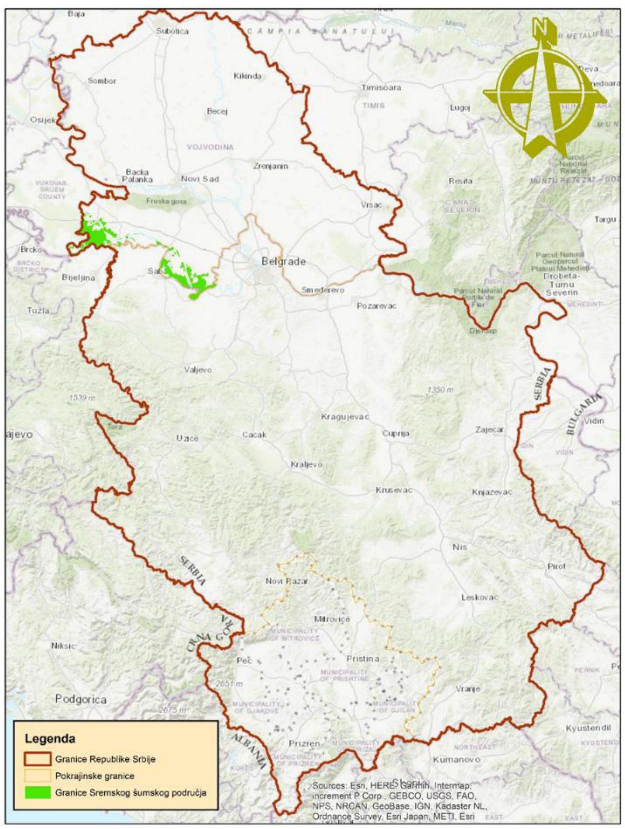

Figure 1. Location of Srem forest areas in Serbia (in green). The north-western area corresponds to Brdoviti Srem forests, and the southeastern area corresponds to Ravni Srem forests.

The Srem Forest District has held a history of forest management by various management systems since 1755 (Bobinac 2008) and currently is managed by Public

Enterprise[1] (PE) "Vojvodinašume". The forest district is not a single, continuous area. Brdoviti Srem is the smaller part in the north that encompasses the southern and eastern slopes of Fruška gora Mountain. Ravni Srem is the larger, southeastern part that encompasses the alluvial terrace along the Sava River, with its individual ponds and canals. The Ravni Srem has undulating terrain with pronounced depressions (canals and ponds) at an elevation of 75–80 m above sea level which experiences high groundwater levels that emerge in spring and autumn filling canals, depressions, and ponds, and drying-up during July and August.

This area experiences a Pannonian steppe, moderate-continental climate. The mean annual temperature is 11 °C. The mean temperature of the coldest month is -0.1 °C, mean temperature of the warmest month is 21.1 °C, and mean temperature during the growing season is 17.6 °C (Babić 2008). The mean annual precipitation is 579 mm, with an average of 344 mm during the growing season (Babić 2008). Based on the "RCP 8.5" climate change scenario of business-as-usual emissions growth (Riahi et al. 2007), the daily average temperature in the Srem area is expected to rise 1.5 to 2 °C, and precipitation is expected to rise about 0 to 10 mm by 2040 (Serbia NAP 2024).

The typical soils of floodplains belong to the FAO systematic units: Fluvisols, Humic Fluvisols, Humic Gleysols (rhyolitic chert), and Gleysols (swamp-gley soil). Soils in the protected areas of floodplains are predominantly heavy and clayey heath loam and meadow loam with unfavorable water and air capacity and a gleyic layer in the lower horizons with the occasional appearance of slatina (waterlogged ground with saline soils) in different stages of development. High groundwater and surface water levels limit the use of seeding across the landscape.

There currently is no significant deforestation in the Srem forest area, other than deforestation for construction of road infrastructure. The more common degradation factors are natural, caused mainly by abiotic factors, i.e., windstorms, drought, or flooding. For example, the windstorm of July 2023 caused damage to 100,000 m^3 of high-quality wood and destroyed 1,300 ha of poplar (*Populus* spp. L.) plantations. Abiotic factors related to moisture availability have a negative impact on existing vegetation in terms of physiological weakening, less frequent fruiting, slower growth, and increased moisture stress. Biotic factors also create disturbance or degrade forests. Oak powdery mildew (*Erysiphe alphitoides* (Griffon & Maubl.) U. Braun & S. Takam.), the oak lace bug (*Corythucha arcuate* Say), and ash dieback (*Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, Hosoya) are currently the most common biotic factors causing natural disturbance in Srem forests. In general, abiotic factors are more significant than biotic factors, in both frequency and intensity.

Pedunculate oak (*Quercus robur* L.) is the dominant species in the Ravni Srem forest, it accounts for about 50% of the standing volume. The most important supporting species in mixed stands are narrow-leaved ash (*Fraxinus angustifolia* Vahl) and common hornbeam (*Carpinus betulus* L.). Even-aged stands 100 to 140 years old dominate the forest, with the number of oak trees ranging between 50 to 120 ha^{-1} and tree heights ranging between 28 to 36 m, depending on stand condition.

Pedunculate oak is a shade intolerant species with a seed crop periodicity of 3 to 5 years in this region. Narrow-leaved ash is somewhat tolerant of low light with a small and easily dispersed seed. In the past, narrow-leaved ash fruited often and

[1] State owned enterprises such as public forests were transformed into joint-stock or limited liability companies in response to a reform policy agreed to with the International Monetary Fund (IMF). PE Vojvodinašume was formed in 2002.

abundantly, but in recent years, due to ash dieback, the seed crop has been gradually reduced and now is completely absent. Common hornbeam, a shade tolerant species, is characterized by abundant seed crops. The most viable and ecologically stable mixed stands of these species are designed with the most rational use of available moisture in the soil, considering that narrow-leaved ash is least plastic, pedunculate oak is moderately plastic, and common hornbeam is most plastic to available soil moisture. Silvicultural practices are applied with regard to the developmental stages of stands, e.g., competition control occurs during stand regeneration and selective high thinning once individuals of dominant tree species attain a height over 17 m and DBH over 25 cm (≈ 25 years old).

In years of a poor or absent acorn crop, seeding is practiced on all areas planned for regeneration. In good mast years, fallen acorns are incorporated into the soil for overwintering by cultivating with a disc implement, or collected and sown mechanically. In the case of mechanical sowing, around 450 kg ha^{-1} of acorns are used, depending on seed viability.

2 Impacts of deforestation or degradation to restoration sites

After deforestation of large areas, especially near settlements, that took place from the late 1880s until the 1950s (Rađević et al. 2020), there has been no significant impact of deforestation or degradation in the Srem forest area. During the 10-year forest regeneration period, there are short-term changes in the hydrological regime of soils and colonization by invasive plants such as *Solidago spp*. L., *Ambrosia artemisiifolia* L., and *Amorpha fruticosa* Thunb. Roe deer (*Capreolus capreolus*) clip terminal buds and red deer (*Cervus elaphus*) peel bark, but this damage is reduced to a minimum by fencing the reforestation areas. Additional causes of damage are abiotic such as early frosts and occasional site flooding and soil waterlogging.

3 Mitigating impacts for seeding

Land leveling, plowing, or ripping are rarely performed, then only if the condition of the soil prevents use of mechanization for seeding. Woody and herbaceous species that can be obstacles to seeding and later oak development are removed. On sites with herbaceous vegetation and woody species of small dimension, competition is removed by mulching and then sites are maintained relatively clear of vegetation using glyphosate-based herbicides. Woody weeds with a DBH over 8 cm are cut with chainsaws. Their stumps are treated with a triclopyr-based arboricide. Seed depredation or damage is caused by feral pigs (*Sus* spp.), wild boar (*Sus scrofa*), rodents (Order Rodentia), pathogenic fungi, and seed insects. Protection is provided by fencing, rodenticides, insecticides, and fungicides. Woven wire fences are built around regeneration areas. Fence height varies between 1.5 to 2.5 m, depending on site conditions. The fence is usually removed after 20 years. Rodenticides are based on zinc phosphide, and the most commonly used fungicides are Falcon (Spiroxamine, Tebuconazole, Triadimenol; Bayer CropScience), Tenor (Propiconazole; Jiangsu Flag), Impact (Flutriafol; FMC), Stroby (Kresoxim-methyl; BASF), and Anvil (Hexaconazole; Syngenta); and insecticides Actara (Thiamethoxam; Syngenta), Laser (Spinosad, Dow Agro Sciences) and Decaguard (Deltamethrin, Gharda Chemicals Limited). Pesticides are applied in line with the Law on Plant Protection Products ("Sl. glasnik RS", br. 41/2009 and 17/2019) and according to labeled instructions from producers.

4 Seed procurement and preparation

Abundant mast crops of oak generally occur every 3 to 5 years. Acorns are collected manually (by hand) by PE employees, local people, and volunteers, in registered seed stands and plantations in autumn (October–November). There are 8 registered seed stands (≈ 645 ha) and 2 seed orchards (≈ 16 ha) for collecting selected Forest Reproductive Material (FRM, as defined in European Union 1999). However, in years with abundant seed crops, the FRM category "source-identified" (as defined in European Union 1999) is also used for seeding. Seed quality is checked by the float method during seed purchase, and it is followed by seed quality testing at a certified institution. After collection, acorns are temporarily stored in a shed before seed processing. Seed processing is conducted with additional float separation, thermotherapy, and fungicide application (Ivetić 2023; Figure 2). Thermotherapy is applied prior to oak seed storage to limit *Ciboria batschiana* (Zopf) N.F.Buchw., one of the major fungal pathogens on stored acorns. Following seed processing, acorns are stored in plastic bags in a refrigerated chamber at 3–5°C for up to one year before sowing.

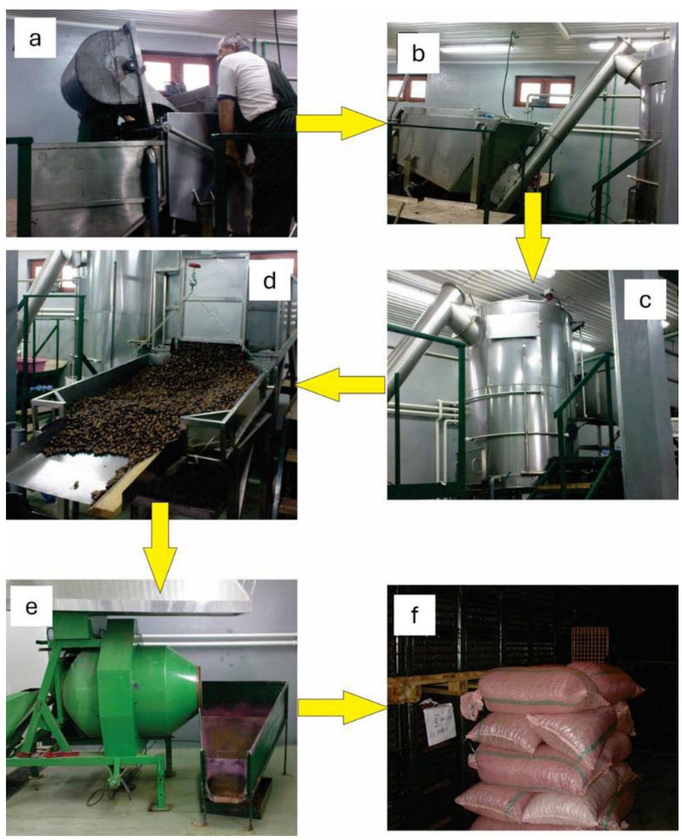

Figure 2. Processing acorns using thermotherapy at the Seed Center in Sremska Mitrovica, Serbia. (a) The acorns are first immersed in water in a perforated drum for separation by floating. (b) The acorns are transferred to the preparation chamber where they are pre-conditioned with water at a 30 to 35 °C. (c) Acorns are transferred by a screw conveyor to the heat treatment chamber, which is filled with hot water from the flow-type boiler room. In this process, the acorns are continuously dosed into the chamber. (d) After 2.5 hours at 41 to 41.5 °C, acorns are spread on a table for drying. (e) After the final heat treatment, the acorns are protected with a fungicide in the drum of an adapted concrete mixer. (f) Treated acorns are stored in a refrigerator facility at 3–5 °C (Photo credits: Vladan Ivetić).

5 Plantation establishment

Regeneration areas are limited to 56.25 ha (the traditionally sized management unit in the Srem Forest Area), with a minimal distance between two regeneration areas of 400 m (PE Vojvodinašume 2023). Before regeneration, all unwanted vegetation is removed, including herbaceous and woody weeds, supporting species, and most oak trees. Typically, 80–100 oak trees ha^{-1} are left in the regeneration area as seed trees, but more for a sheltering role rather than as a source of seed. These trees are removed once 70-80% of regeneration area is regenerated (naturally, by direct seeding or by their combination) with 2-5 well developed seedlings per square meter, usually after 3-5 years, but depending on specific conditions, this period can be extended up to 10 years. Pedunculate oak is the primary species seeded, while the supporting species naturally occupy the site. Sowing is done in the autumn–winter with mechanical seeding machines (Figure 3). About 450 kg ha^{-1} of acorns are sown at 2 to 5 cm deep in rows 0.7 m apart and acorns spaced 15 to 20 cm in a row (Figure 4). When acorns are sown immediately following collection, they are not treated in any way. Acorns stored following thermotherapy are treated with the fungicide VITAVAX-200 ff (Carboxin+Thiram; Chemtura), prior to storage. In any case, there is no need for additional stratification or pre-sowing treatment of acorns.

Figure 3. A tractor-drawn sowing machine being loaded with acorns (Photo credits: PE “Vojvodinašume”).

Figure 4. Pedunculate oak (*Quercus robur* L.) seedlings on a regeneration area after the first growing season (Photo credits: PE “Vojvodinašume”).

6 Post-sowing practices and maintenance

Early competition control is accomplished with herbicides. If competing vegetation establishes before oak germination, directed spraying of glyphosate is used for control. If oak germination has occurred, selective herbicides are used to control competition, e.g., Nikogan (Nicosulfuron; Syngenta); Pulsar (Imazamox; BASF); and Lontrel (Clopyralid; Corteva). The tending of oaks is performed during the sapling phase of development, with mechanical weed control using hand tools (Figure 5). Regeneration sites are fenced to protect acorns, seedlings, and saplings from animal damage, and they are protected from fire with established fire lanes or strips. The fire lanes are maintained by tilling for up to 15 years after initiation of regeneration.

Figure 5. Manual weeding in regenerated pedunculate oak (*Quercus robur* L.) in an early stage (Photo credits: PE "Vojvodinašume").

7 Successful seeding

There are three pillars of reforestation success through seeding in the Ravni Srem forest area. 1) Application of established and proven reforestation technology, based on knowledge of the biology of pedunculate oak and supporting species, and developed from experience from previous trials. 2) Implementation of reforestation efforts are timely and supported by technical and financial resources. 3) The Forest District receives the support and understanding of the community. This is achieved through education and outreach by forestry professionals participating in media opportunities.

Regeneration success is assessed by mapping establishment and survival after the first growing season. The regenerated area is divided into working plots (60 x 150 m) and in each working plot, sample plots are established; 2–4, 10 m^2 plots in homogenous conditions or 6–8 sample plots in heterogenous germination conditions. Inside sample plots, seedlings meeting a 15 to 30 cm height criterion are counted, and there should be at least 1 established seedling per 1 m^2 (the usual number is 2 to 5). In the establishment phase, reforestation is considered successful if oak seedlings originating from seeding show good survival and are well developed, and supporting species are present in the stand as well. The primary reasons for failure are unfavorable climatic factors, including high groundwater and surface water levels.

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This paper may include research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All use of pesticides must be registered by appropriate agencies before they can be recommended.

CAUTION

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

9 References

Babić V (2008) Climate characteristics of Srem area. Šumarstvo 60(4):99–108.

Banković S, Medarević M, Pantić D, Petrović N (2009) National Forest Inventory of the Republic of Serbia: Forest Fund of the Republic of Serbia (1st ed). Ministry of Agriculture, Forestry and Water Management of the Republic of Serbia, Forest Administration.

Bobinac M (2008) Obnavljanje šuma u vreme Petrovaradinske Imovne opštine i šumsko-poljsko gazdovanje. In: Tomović Z (ed) 250 godina šumarstva Ravnog Srema, Sremska Mitrovica: Javno preduzeće 'Vojvodinašume' - Šumsko gazdinstvo Sremska Mitrovica, str, pp 119–126.

European Union (1999) Council Directive 1999/105/EC of 22 December 1999 on the marketing of forest reproductive material. THE COUNCIL OF THE EUROPEAN UNION, Official Journal L 011, 15/01/2000, pp 17–40.

Ivetić V 2023 Forest Reproductive Material – Biology and Technology of Production of Forest Trees Seed and Seedlings (In Serbian). University of Belgrade – Faculty of Forestry – University book, Belgrade, Serbia.

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. For Ecol Manag 448:474–489. https://doi.org/10.1016/j.foreco.2019.06.032

NFI (2023) National Forest Inventory of Republic of Serbia – complete results. Available at: https://upravazasume.gov.rs/wp-content/uploads/2023/12/Complete_Results_Serbia_27-11-2023.xlsx (last accessed 21 February 2025).

PE Vojvodinašume (2023) https://www.vojvodinasume.rs/wp-content/uploads/2023/07/01_Smernice_obnova-visokih-suma.pdf (last accessed 19 December 2024).

Rađević V, Pap P, Vasić V (2020) Management of the common oak forests in Ravni Srem: Yesterday, today, tomorrow. Topola 206:41–52. https://doi.org/10.5937/topola2006041R

Republic of Serbia (2010) First national report of the Republic of Serbia to the United Nations Convention on Biological Diversity. Ministry of Environment and Spatial Planning. https://www.cbd.int/doc/world/rs/rs-nr-01-en.pdf

Riahi K, Gruebler A, Nakićenović N (2007) Scenarios of long-term socio-economic and environmental development under climate stabilization. Technol Forecasting Social Change 74:887–935. https://doi.org/10.1016/j.techfore.2006.05.026

Serbia NAP (2024) Digital Climate Atlas of Serbia. https://atlas-klime.eko.gov.rs/ (last accessed 19 December 2024)

Seeding forest trees

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Abstract

Seeding is gaining popularity in global forestation for its scalability and cost-effectiveness, especially where nursery stock is limited. It enables rapid, large-scale forest establishment, even on remote or degraded sites, and allows control over species and genetic diversity. Seeding is cost-effective for inaccessible or low-productivity areas and is used in ecological restoration to boost biodiversity. Success depends on species, seed quality, timing, soil, and site management. It is best suited for areas where natural regeneration is infeasible, low-cost forestation is needed, sites are remote or difficult to access, or rapid resource control is required. Germination and establishment rates are generally low (average germination ~44%, establishment ~21%), with significant variability by species and site. Large-seeded, fast-germinating species perform better. Seed availability and quality are key challenges. Proper timing, storage, and site preparation are crucial, particularly for species with recalcitrant seeds. Methods include broadcast and direct placement, with drone seeding emerging for large projects. Higher seeding rates are needed for small seeds and broadcast methods. Climate change is increasing drought and heat stress, making moisture retention and microclimate management more important. Technological advances, like automation, seed treatments (coatings, biochar, mycorrhizal inoculation and encapsulation), and precision seeding, are improving outcomes. Combining seeding with planting can enhance diversity and success, but careful planning and ongoing management remain essential.

Keywords

direct seeding, forest restoration, seed quality, species selection, seed predation, technological innovations, establishment rates

Contents

1 Introduction

Globally the interest in forestation, including large-scale tree planting initiatives, has surged but the demand for forest reproductive material (seeds, cuttings, whole plants) cannot be satisfied only by planting stock from nurseries (Bannister et al. 2018; Fischer et al. 2016; Naruangsri et al. 2024; Nunes et al. 2020). Thus, seeding has regained interest because of its scalability and potential cost-effectiveness (Grossnickle and Ivetić 2017; Pedrini and Dixon 2020). Seeding (sowing, direct seeding) disperses tree seeds directly into an area for forestation. Seeding can be applied quickly, over large areas, and on inaccessible sites; despite these advantages, seeding fell out of favor due to its unpredictability (Oliet and Jacobs 2012; Palma and Laurance 2015).

Seeding is not a new technique for establishing forests, dating back at least to the Middle Ages (Willoughby et al. 2004). Prior to early 1900s, seeding was uncommon in the USA but practiced in northern Europe; for example, in Scandinavia, more than one-fourth of the artificial regeneration was by seeding (Toumey 1916). Nevertheless, there was little consensus among foresters as to its effectiveness, but it was clear that the best results were on good sites without competing vegetation; other factors for low success were lack of site preparation and poor seed quality (Toumey 1916). Seeding of heavy-seeded species such as *Quercus* L. acorns was practiced by Indigenous people for centuries to produce a food source (Abrams and Nowacki 2008; Gil-Pelegrín et al. 2017) and persisted as the most common artificial regeneration method for these species by foresters through the early 20th Century for timber and wildlife benefits (Löf et al. 2019). In most developed countries since the 1970s, however, seeding has been a minor component of forestation programs. Conversely, broadcast and direct seeding are used on a much larger scale in the tropics, especially in China, Vietnam, and India (Grossnickle and Ivetić 2017; see Wang et al. (2026) this issue).

2 Advantages of seeding

Seeding, particularly direct seeding, overcomes some of the limitations of natural regeneration. Plants are extremely sensitive and vulnerable in the earliest phase of forestation when seeds germinate, and seedlings begin development (Oliver and Larson 1996). In natural regeneration of some species, this vulnerability is compensated for by repeatedly dispersing enormous amounts of seed over the years (Grubb 1977). Seeding is not limited to local seed sources and offers some control over the species composition and genetic quality of the forestation. This advantage of seeding is realized when the sources of reproductive material lack desirable species or any sources at all. In large areas of former farmland, pastureland, and burned areas, local seed sources are too distant for effective dispersal (Gardiner and Oliver 2005; Stanturf et al. 1998). Similarly, when site conditions are inhospitable for desired local species, abiotic or biotic obstacles (e.g., acidic spoils or subsoil on mined land, sites overtaken with rank weed species, or subject to heavy ungulate browsing) could be overcome by establishing species better adapted to site conditions (e.g., Madalcho et al. 2025; Madsen et al. 2015). Even where seed sources are present, the available sources may be limited to less-desirable species. In the tropics, where natural regeneration is effective, the loss of seed-dispersing animals (defaunation) can result in sites dominated by a few pioneer tree species, limiting recovery of tree species richness and biodiversity (Cole et al. 2011; Egerer et al. 2018; Naruangsri et al. 2024).

The primary advantage cited for preferring seeding over planting seedlings largely is due to lower cost. As Bullard et al. (1992) pointed out, however, this is true only when seeding is successful. Thus, seeding can be cost effective compared to planting remote and inaccessible areas where transportation and labor costs are excessive (see Wang et al. (2026) and Sudrajat et al. (2026) in this issue), on severely degraded sites where commercial species are not adapted nor economically viable, simply when seeding is likely to be successful and less expensive than planting (e.g., Baumhauer et al. 2005), or in protected areas where planting is prohibited (see Pansing and Tomback (2026) in this issue). Seeding has been used effectively for afforestation, reforestation, and restoration, especially for establishing large-seeded species that do not disperse readily such as *Quercus* spp. (Löf et al. 2019) and *Fagus sylvatica* L. (Ammer and Mosandl 2007). Seeding has also gained favor over planting in ecological restoration for establishing mixed species stands (Grossnickle and Ivetić 2017). In Brazil, for example, the *muvuca* method uses seeds of native trees and perennial/sub-perennial green manure species that are delivered in an inert material such as sand, saw dust, or mineral soil with a lime or grass seed spreader (Campos-Filho et al. 2013; and see Engel et al. (2026) in this issue).

Grossnickle and Ivetić (2017) summarized guidance from multiple sources and described situations in which seeding could be an attractive forestation option, including the following:

- Where natural regeneration is infeasible, including afforestation of large abandoned agricultural sites and mine reclamation projects or disturbed areas where natural regeneration is inadequate. This includes sites where rapid reforestation or restoration is needed, such as large areas that result from wildfire or other natural disasters, to give the desired tree species an opportunity to reestablish the site before development of competing vegetation.
- When low-cost forestation is needed, including low-productive or disturbed sites where the cost of planting operations is not economically feasible or in low-budget restoration programs addressing conservation and recovery of forest ecosystems.
- When other considerations are important, such as sites are remote or inaccessible or sites have rocky soils making it difficult to plant seedlings, there is a limited availability of bareroot or container-grown seedlings, and in enrichment seeding of late successional species in established forests to increase species diversity.
- Where there is a need in agroforestry to rapidly control site resources and direct them away from weed species and towards the agricultural crop and tree species.

3 Seeding success

Although seeding can be a cost-effective method for forestation, it requires careful planning and execution to maximize the chances of success, requiring more than just seed delivery to the site; it is a comprehensive process requiring many silvicultural factors to ensure program success (Grossnickle and Ivetić 2017). Toumey (1916) summarized the factors to consider to ensure successful seeding: (1) tree species and seed quality, (2) timing of seeding, (3) depth of covering, (4) soil conditions, (5) vegetative cover, and (6) seed predation. These are still the most important factors controlling seeding success (Grossnickle and Ivetić 2017), as substantiated in the papers in this journal issue. Selecting appropriate species is critical and success can depend on seed traits such as size, dormancy, tolerance to desiccation, and storage behavior.

4 Species and seed quality

Seeding has a low rate of success in general, in terms of germination, establishment, and growth (Ceccon et al. 2016; de Souza and Engel 2023; Grossnickle and Ivetić 2017; Palma and Laurance 2015). Grossnickle and Ivetić (2017) found an overall average germination rate for seeding of 44% (range 9% to 92%). The average germination rate was 38% for tropical species, 47% for temperate hardwoods, and 46% for temperate conifers. The establishment rate, defined as survival rate after at least one growing season per total number of seeds sown, across all studies was 21% (range 0% to 92%). The average establishment rate was 17% for tropical species, 28% for temperate hardwoods and 16% for temperate conifers. The variability of successful seeding is due to seeding practices (including timing, site preparation, sowing depth), site conditions, seed predation, and vegetation competition (Ceccon et al. 2016; de Souza 2022; de Souza and Engel 2023; Grossnickle and Ivetić 2017). In addition, seedlings established through seeding grow slower than planted seedlings on sites with competing vegetation.

The collective experience reported in this journal issue supports the several reviews mentioned above. Aerial seeding of high numbers of seed of *Pinus massoniana* Lamb. in China (350,000 to 540,000 ha^{-1}) resulted in 1% establishment (see Wang et al. (2026) in this issue). Similarly, broadcast seeding of *Pinus sylvestris* L. in the Mediterranean region was low, from 0% to 5% with some reports of higher rates (see Castro et al. (2026) in this issue). Germination and establishment rates were much higher with fewer seeds sown in seeding, where seeds were buried, such as for *Quercus* spp. in Sweden, Serbia, Mexico, and the southern United States (see Löf et al. (2026), Ivetić and Marinković (2026), López-Barrera and García-Hernández (2026), and Gardiner and Stanturf (2026) in this issue). Encapsulation in a briquette and burial produced germination and survival rates greater than 50% for several species in Indonesia (see Sudrajat et al. (2026) in this issue). These authors noted the need to adjust depth of burial by the size of seed, as cited by Grossnickle and Ivetić (2017).

Tree species suitability for seeding share certain characteristics of stress tolerance, fast germination, establishment and initial growth, and some shade tolerance (Tunjai and Elliott 2012). Thus, early-successional and pioneer species with the ability to grow rapidly, and late-successional and climax tree species with large seeds and food reserves should be good choices among local species (Ceccon et al. 2016; Grossnickle and Ivetić 2017; Palma and Laurance 2015) (Figure 1). Nevertheless, small seeds and seeds with low water content could be better adapted to seeding in dry regions as they are less susceptible to desiccation. Smaller seeds are better for broadcast seeding as they have the potential to enter disturbed soil or sites with some grass cover (Grossnickle and Ivetić 2017). Seed quality is important; low quality and viability of collected seeds and poor storage procedures can lead to seeding failure (Merritt and Dixon 2011). The lack of information on seed phenology, development, and maturation for tropical species can result in inappropriate timing of seed collection, affecting quality and viability that cannot be overcome by simply sowing more seeds (see Engel et al. (2026) this issue).

In addition to the effects that seed quality have on seeding success, seed collection, handling, and storage effects on quality have broader implications for efforts to sow multiple species to establish biodiverse stands. Seed collection and handling are the highest costs in seeding operations (see Castro et al. (2026) and Pansing and

Tomback (2026) in this issue). Particularly in tropical systems where very high seeding rates are typical (e.g., 101,000–500,000 seeds ha^{-1} in Brazil (de Souza and Engel 2023; Freitas et al. 2019), the availability of seed is a bottleneck in scaling up restoration (de Souza and Engel 2023). Achieving satisfactory tree seedling density and ground coverage for recalcitrant species requires sowing immediately after seed collection. Nevertheless, seeds of different species need to be collected throughout the year, which require storage, awaiting favorable germination conditions during the rainy season (Vieira et al. 2008), or simply to obtain seeds of enough species to sow simultaneously (de Souza and Engel 2018; and see Engel et al. (2026) in this issue). Seed loss by inappropriate storage conditions could mean species with recalcitrant seeds that disperse seeds during the dry season would be lost for sowing during the rainy season.

The timing of seeding is important in some ecosystems (Grossnickle and Ivetić 2017; Toumey 1916). The best time for seeding is when site conditions are optimal for germination and establishment, typically when there is plentiful moisture, temperature is optimum, there is minimal weed competition, and a potentially favorable growing season before exposure to stressful environmental conditions (Schmidt 2008). Climate introduces considerable variation in these conditions, for example in timing of rainy seasons in the tropics (see Sudrajat et al. (2026) this issue) or autumn versus spring seeding in boreal and temperate biomes (Grossnickle and Ivetić 2017). Climate change is affecting 'normal' conditions producing even more uncertainty (Grossiord et al. 2020; Johnston et al. 2025; Novick et al. 2024; and see Castro et al. (2026) in this issue).

Figure 1. Some birch (*Betula* spp. L.) species are relatively fast-growing pioneer trees that have been successfully seeded where disturbance has exposed bare soil on the site (Photo credit: Skyseed GmbH, Germany).

Orthodox seed can be dried to a constant moisture and stored for extended time, but recalcitrant seed remain hydrated at maturity, are easily damaged by drying, and typically cannot be stored for long periods. Useful information on seed characteristics and storage and germination requirements can be found in local sources and several international manuals (Bonner and Karrfalt 2008; Pedrini et al. 2020b; Schmidt 2016; Vozzo 2002). Some innovative seed delivery systems like seed pellets and briquettes or coatings with substances such as biochar or hydrogels can be used to enhance moisture retention, germination, and protect seeds from harsh environmental conditions (Pedrini et al. 2020a; Stanturf et al. 2024; and see Castro et al. (2026) and Sudrajat et al. (2026) in this issue). Other measures are used to treat seed before sowing to speed up breaking dormancy of some seed. Seed priming is a pre-germination treatment that partially hydrates seeds to activate early metabolic processes, without allowing seed to fully germinate. Accelerating germination is one way to reduce losses to seed predators (see López-Barrera and García-Hernández (2026) in this issue), a major reason for losses and low germination rates (Witzell et al. 2026). Various measures have been evaluated to minimize seed predation by rodents and other animals, potentially using techniques like repellents (e.g., capsaicin) or physical protection such as tubes and cages (Stanturf et al. 2024; Witzell 2026). Doubling the seeding rate for the first 30 m beyond a forest edge is suggested to overcome predation, as well as protecting animals in the vicinity that prey on seed predators. Seed predators probably detect seed in several ways, but mainly by vision and smell. For some species and at some sites covering or burying seed seems to be the most effective deterrent to predation, but it may not work in all instances.

5 Seedbed receptivity

Seedbed receptivity (Balandier and Prévosto 2015; Toumey 1916) is a combination of soil characteristics and vegetative cover, in concert with seed characteristics that determine optimum sowing depth. Broadcast seeding, however, has the advantage of efficiently covering a large area as well as providing a means to seed remote areas and difficult terrain (Schmidt 2008; and see Lord and Moss-Mason (2026) and Wang et al. (2026) in this issue) and a feature of drone seeding that is much in vogue (Amorós and Ledesma 2020; Saldarriaga et al. 2025; Stanturf et al. 2024) (Figure 2). The disadvantage of broadcasting is that seeds lie on the ground, exposing them to harsh environmental conditions, which can result in very low establishment rates (Grossnickle and Ivetić 2017). Broadcast seeding typically requires higher rates than direct seeding, which is often conducted in rows (line seeding) or at predetermined seeding spots, as noted by Castro et al. (2026) in this issue. However, broadcast seeding when combined with proper site and seedbed preparation and vegetation control can be a successful practice (Brooks et al. 2009).

Control of competing vegetation, commonly grasses (Poaceae), forbs, and shrubs, is required to ensure the proper environment of light, soil moisture, and available nutrients for seeds to germinate and germinants to survive and grow (Aguirre-Salcedo et al. 2025; Bonilla-Moheno and Holl 2010; Dias Laumann et al. 2023; Doust et al. 2006; Grossnickle and Ivetić 2017; Guariguata 2000; Kildisheva et al. 2020; Laumann et al. 2023). Existing shrub and grass vegetation and relatively mild drought stress interferes with forestation efforts that usually succeeds better after removing or avoiding this vegetation (Witzell et al. 2026). Not all existing vegetation should be considered competition, however, especially in drier climates where existing vegetation can ameliorate harsh conditions and serve as nurse plants (Brooker et al. 2008; García et al. 2000; Gómez-Aparicio et al. 2004; Tanner et al. 2025; and see Castro et al. (2026) in this issue).

Figure 2. An aerial drone used to efficiently broadcast seed at forestation sites that are remote or of difficult terrain (Photo credit: Skyseed GmbH, Germany).

Soil degradation, compaction, and loss of organic matter often limit seeding success (Stanturf and Callaham 2021). Afforestation on abandoned farmland may face vigorous competition from existing vegetation, depending on how long the site was abandoned from active management. In South America and New Zealand former pastureland offers the most opportunities for seeding (Camargo et al. 2002; Cole et al. 2011; de Souza and Engel 2023; and see Lord and Moss-Mason (2026) in this issue). Past land use practices leave these soils compacted, nutrient-depleted, and low in water retention capacity (Foley et al. 2005). Site preparation is needed to facilitate tree establishment (Löf et al. 2012; Löf et al. 2015) but using heavy equipment should be carefully managed to prevent further soil compaction. Former land use can also improve site conditions. Freitas et al. (2019) compared success of species mixtures seeded by different methods (broadcast, row seeding, spot seeding) with intense site preparation. Broadcast did best and sites with higher soil phosphorus (P) content had more tree density, basal area, and biomass compared to the others. In addition, both aboveground biomass and tree height increased with soil base saturation. The great variation in phosphorus content was due to previous land use; high-P sites were formerly in grain production and received lime and fertilizer.

Mechanical site preparation (MSP) improves microsites and increases the efficiency of the seeding procedure (Löf et al. 2012; Sikström et al. 2020). Methods for soil preparation vary with region, knowledge, traditions, cost, and available machinery (Figure 3). Conventional MSP usually involves displacing the topsoil layer into spots, patches, or strips, to remove weeds or disrupt compaction or impeding layers (e.g., iron pans, calcrete, plow pans) that prevent the penetration of water and roots. Other soil amendments such as manure, fertilizer, or biostimulants can be applied at the same time (Stanturf et al. 2024; Witzell et al. 2026). Site preparation to control competing vegetation was a common theme in the papers in this journal issue. Similarly, managers in the western United States selected recent wildfire burned areas for seeding *Pinus albicaulis* Engelm. in remote mountainous areas (see Pansing and Tomback (2026) in this issue).

Figure 3. A tractor-drawn mechanical seeder used to prepare the seedbed in a Norway spruce (*Picea abies* (L.) H. Karst.) plantation and sow a seed mix of desired species directly into the row of prepared soil (Photo credit: Palle Madsen).

Climate change complicates seedling establishment by increasing the frequency and intensity of stressors such as drought and heat waves. Rising temperatures accelerate seedling water loss through transpiration due to drying of the air (i.e., vapor pressure deficit), making soil moisture conservation and microclimate management critical (Grossiord et al. 2020; Novick et al. 2024). Site preparation should prioritize moisture retention on dry sites to mitigate these risks by incorporating cover cropping, mulching, and water-retaining amendments (Stavi et al. 2024; Stavi et al. 2020; Vallejo et al. 2012). The same benefits are obtained by facilitation from shrubs and herbaceous species (see Castro et al. (2026) and Lord and Moss-Mason (2026) in this issue), sheltering leave trees after clearcutting (see Ivetić and Marinković (2026) in this issue), and by judicious selection of microhabitat (see Pansing and Tomback (2026) in this issue). On wet sites such as many boreal sites, however, MSP is used to get rid of excess moisture, for example by mounding that creates a drier site with higher soil temperatures during the growing season.

6 Seeding methods

Broadcast seeding is done by hand or mechanical devices on the ground or aerially by fixed wing aircraft, helicopters, and more recently by drones. Seeding places seed (by hand or mechanically) into strips, lines, holes, or spots (Grossnickle and Ivetić 2017; Toumey 1916). Both seed delivery methods benefit from site preparation that can be as simple as soil scarification or intensive ripping and plowing (Löf et al. 2012; Löf et al. 2015; Witzell et al. 2026). Seeding by drones equipped with specialized seed-dispersers is an innovative technique for large-scale forestation projects (Stamatopoulos et al. 2024; Stanturf et al. 2024; Tiansawat and Elliott 2020). Advanced drone systems can be programmed to distribute seeds evenly and in appropriate densities. Drones can deliver seed mixes encapsulated in seed balls and can sow coated seeds (Stanturf et al. 2024; Witzell et al. 2026). The survival of the seedlings after germination may, however, still be a significant challenge.

Correct sowing depth, spacing, and seeding rates are vital for successful germination and establishment. Seed burial, versus broadcast seeding, was found to improve establishment rates (Doust et al. 2006; Garcia-Orth and Martínez-Ramos 2008; Negreros-Castillo et al. 2003; Woods and Elliott 2004). Typically, the best seeding depth depends on seed size. Though there are general rules for proper sowing depth, there is enough inconsistency to show that species and site conditions ultimately dictate seeding practices. Seed burial to depths ideal for the species involved will lessen desiccation and protect against predation (Doust et al. 2006; Garcia-Orth and Martínez-Ramos 2008). A general rule is that seeding depth is between one and two times the seed width (Grossnickle and Ivetić 2017). Site conditions, such as soil quality, competition from weeds, predation pressure, and moisture availability influence establishment success, and therefore the necessary seeding rate (Figure 4). Precision seed drilling machines are being evaluated in the Mediterranean region and New Zealand (see Castro et al. (2026) and Lord and Moss-Mason (2026) in this issue).

Figure 4. Seed predation and herbivory to young seedlings can influence establishment success on some restoration sites such as this pedunculate oak (*Quercus robur* L.) plantation that was fenced to exclude some herbivores. (Photo credit: Magnus Löf).

7 Seeding rates

Tree species have different seed sizes, germination rates, and establishment requirements. Hard mast species like *Quercus* spp. or *Fagus* spp. L. often have lower seeding rates compared to light-seeded species such as *Pinus* spp. L., *Acer* spp. L., or *Fraxinus* spp. L. (Grossnickle and Ivetić 2017). Using high-quality, viable seeds with good germination rates reduces the need for excessively high seeding rates. The target number of established trees per ha and field germination rates dictates the initial seeding rate. Some recommended seeding rates are 6,250-10,000 seeds ha^{-1} for species planted in rows. Higher rates are suggested for broadcasting, ranging from 12,500-37,500 seeds ha^{-1} (Grossnickle and Ivetić 2017) although even higher rates, from

100,000 to 500,000 seeds ha^{-1}, have been used (Freitas et al. 2019; and see Castro et al. (2026) and Wang et al. (2026) in this issue).

8 Final thoughts

Seeding shows high variability across species and sites, with meta-analyses and large field trials demonstrating that establishment rates are typically low (often <20% of seeds sown), but are consistently higher for species with large seeds, rapid germination, and storage cotyledons (Ceccon et al. 2016; Freitas et al. 2019; Grossnickle and Ivetić 2017). Nevertheless, seeding small seeded species can be successful, particularly with adequate site preparation and competition control (e.g., Willoughby and Jinks 2009; Willoughby et al. 2004; Willoughby et al. 2019; and see Castro et al. (2026), Wang et al. (2026), and Pansing and Tomback (2026) in this issue). Trait-based selection (favoring large-seeded, fast-germinating, storage cotyledon species) offers practical decision support for improving early establishment (Piotrowski et al. 2023), though long-term stand development may equalize some initial species differences. There is often a strong positive effect of seed mass on seeding success, confirmed in global meta-analyses, tropical and temperate field trials, and trait-based syntheses (Bonilla-Moheno and Holl 2010; Ceccon et al. 2016; de Souza 2022; Downer et al. 2024; Freitas et al. 2019; Grossnickle and Ivetić 2017; Hankin et al. 2023; Löf et al. 2019; Lozano-Baez et al. 2025; Madsen and Löf 2005; Naruangsri et al. 2024; Negreros-Castillo et al. 2003; Palma and Laurance 2015; Tunjai 2012; Waiboonya and Elliott 2020; Willoughby et al. 2019).

Increasing demand for forestation has renewed interest in seeding as a low-cost method. Technological innovations, particularly in the fields of automation and precision seeding, enable large-scale seed dispersal in previously inaccessible or degraded areas (Castro et al. 2021; Liu et al. 2023; Mohan et al. 2021). Seeding is more suitable for remote or inaccessible areas, sites with low productivity where planting seedling costs are prohibitive, or when aiming for a more natural forest structure (e.g., see Lord and Moss-Mason (2026), Sudrajat et al. (2026), and Wang et al. (2026) in this issue).

Seeding alone, or in combination with planting seedlings, can produce biodiverse forest restoration (see Engel et al. (2026) in this issue). To maximize biodiversity in forest regeneration – whether by planting, seeding, or a combination – it is key to include a wide range of species adapted to the local environment and climate. Assuming continued and proper management, species richness is promoted by incorporating a high number of species to increase the overall diversity of the regenerating forest (see Gardiner and Stanturf (2026) and Lord and Moss-Mason (2026) in this issue). Functional diversity is enhanced by selecting species with different ecological functions, such as early successional pioneers, nitrogen-fixers, and shade-tolerant late successional species. Restoration methods such as the framework species method (Elliott et al. 2013; Elliott et al. 2023) and *muvuca* (Campos-Filho et al. 2013) seek to implement these considerations. This also contributes to spreading (reducing) the risk of total failure of a seeding operation and increases the chance that at least one or more species establish.

Seeding is not appropriate for meeting all forestation objectives. Planting seedlings is preferred when predictable success rates, uniform spacing, faster growth, and better control over the regeneration process are priorities. Nurseries and nursery techniques were invented and implemented for good reasons. Combining seeding and planting can be advantageous for some situations, such as planting target species and seeding 'sacrificial' nurse species (Witzell et al. 2026; and see Lord and Moss-Mason (2026) in this issue) or to increase diversity. Seeding can facilitate the introduction of a greater diversity of species compared to traditional planting, particularly at lower cost than attempting the same level of diversity by only planting seedlings. Seeding also can create conditions with many seedlings, which can be an advantage for quality timber production (by producing many stems from which to select a quality stem or by shading the boles of target species to prevent sprouts that reduce timber quality). Ultimately, the best method depends on the specific site conditions, species selection, available resources (especially sufficient quality seed), and desired outcomes for the forestation project.

Seeding is generally cheaper than planting seedlings as it avoids nursery and planting labor costs, but this is true only if seeding is successful (e.g., Bullard et al. 1992). Broadcast or direct seeding allows for rapid coverage of extensive areas, especially after disturbances like wildfires, but is also likely to suffer from low establishment rates. Trees established from seeding tend to develop natural and unrestricted root systems when sown in properly prepared seedbeds, potentially leading to better stability compared to planted seedlings whose roots can become distorted in pots or during planting (e.g., compared to polybags; see Sudrajat et al. (2026) in this issue). Although, using quality seedlings and good planting techniques reduces any root development abnormalities.

Limitations of seeding, especially by broadcasting, should be considered. Seeding gives reduced control over spacing and stocking. Achieving optimal spacing and density can be challenging with seeding, potentially leading to overcrowding or insufficient tree numbers. While this may be a drawback in timber production systems, it may be an advantage for biodiversity objectives. Longer rotation times and lower yields are typical of seeded compared to planted stands due to slower early growth rates. Seeded stands may take longer to reach maturity compared to planted seedlings, potentially leading to lower timber values. Nevertheless, seeding can be used when natural regeneration is compromised by non-mast years (see Ivetić and Marinković (2026) in this issue).

Early seedling mortality can be higher with seeding due to factors like herbivory, seed predation, competition from weeds, drought, and frost as new germinants are more fragile compared to nursery stock. A more significant problem is that seeding requires large quantities of seed to offset high mortality rates. Availability of seed, particularly of heretofore non-commercial species, in many regions reduces the ability to restore diverse native forests (Bannister et al. 2018; de Souza and Engel 2023; Frischie et al. 2020; Pedrini et al. 2020b; and see Engel et al. (2026) and Pansing and Tomback (2026) in this issue).

Improvements in the application of seeding for forestation programs are needed to create more effective seed dispersal, increase seedbed receptivity, minimize seed predation, or create a more favorable microsite environment (Grossnickle and Ivetić 2017; Palma and Laurance 2015; Shaw et al. 2020). Advances in seed pre-treatment and encapsulation techniques potentially should improve germination rates and better protect seeds from environmental stresses and seed predation (Pedrini et al. 2020a; Pedrini et al. 2020b; Shaw et al. 2020). These include seed coating, biochar infusions, and mycorrhizal fungi inoculation (Stanturf et al. 2024; and see Castro et al. (2026) and Sudrajat et al. (2026) in this issue).

Seeding is operationally feasible for multi-species forest restoration but typically yields low (<20%) conversion from seed to established stem, with marked species and site variability. Post-emergence survival, not just high germination, is a key bottleneck; sites and treatments with high initial emergence can still see strong attrition, especially under competitive or drought stress. There is a pronounced move toward comparing a broad array of species, especially evaluating trait-based predictions and community assembly outcomes. Management interventions (site manipulation, microtopography, ground cover, protection), novel seed treatments (biochar, coatings), and species selection tailored to traits and function can improve initial emergence and survival, but success frequently depends on manipulating the local abiotic and competitive environment. The contributions by author in this journal issue illustrate some of the work underway to improve seeding success.

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10 References

Abrams MD, Nowacki GJ (2008) Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. The Holocene 18(7):1123–1137. https://doi.org/10.1177/0959683608095581

Aguirre-Salcedo C, Montaño-Arias SA, Jansson R (2025). Restoration implications of the germination ecology of six dry-forest woody Fabaceae species in Mexico. Trees 39(2):33. https://doi.org/10.1007/s00468-025-02606-0

Ammer C, Mosandl R (2007). Which grow better under the canopy of Norway spruce—planted or sown seedlings of European beech? Forestry 80(4):385–395. https://doi.org/10.1093/Forestry/cpm023

Amorós L, Ledesma J (2020) Aerial robotics and forest management and seeding. In: Elliott S, Gale G, Robertson M (eds) Automated Forest Restoration: Could robots revive rain forests? Proceedings of a brain-storming workshop, FORRU-CMU, Chiang Mai University, Chiang Mai, TH, pp 102-111.

Balandier P, Prévosto B (2015) Forest restoration in the French Massif Central Mountains. In: Stanturf JA (ed), Restoration of Boreal and Temperate Forests, Second Edition, CRC Press, Boca Raton, FL, USA, pp 337-354.

Bannister JR, Vargas-Gaete R, Ovalle JF, Acevedo M, Fuentes-Ramirez A, Donoso PJ, Promis A, Smith-Ramírez C (2018) Major bottlenecks for the restoration of natural forests in Chile. Restor Ecol 26(6):1039–1044. https://doi.org/10.1111/rec.12880

Baumhauer H, Madsen P, Stanturf J (2005) Regeneration by direct seeding—a way to reduce costs of conversion. In: Stanturf JA, Madsen P (eds) Restoration of Boreal and Temperate Forests. CRC Press, Boca Raton, FL, USA, pp 349–354.

Bonilla-Moheno M, Holl KD (2010) Direct seeding to restore tropical mature-forest species in areas of slash-and-burn agriculture. Restor Ecol 18(s2):438–445. https://doi.org/10.1111/j.1526-100X.2009.00580.x

Bonner FT, Karrfalt RP, eds (2008) The Woody Plant Seed Manual. US Department of Agriculture Forest Service, Agriculture Handbook 727, Washington, DC, USA.

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JMJ, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz CL, Saccone P, Schiffers K, Seifan M, Touzard B, Michalet R (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96(1):18–34. https://doi.org/10.1111/j.1365-2745.2007.01295.x

Brooks S, Cordell S, Perry L (2009) Broadcast seeding as a potential tool to reestablish native species in degraded dry forest ecosystems in Hawaii. Ecol Restor 27(3):300–305. https://doi.org/10.3368/er.27.3.300

Bullard S, Hodges JD, Johnson RL, Straka TJ (1992) Economics of direct seeding and planting for establishing oak stands on old-field sites in the South. South J Appl For 16(1):34–40.

Camargo JLC, Ferraz IDK, Imakawa AM (2002) Rehabilitation of degraded areas of central Amazonia using direct sowing of forest tree seeds. Rest Ecol 10(4):636–644. https://doi.org/10.1046/j.1526-100X.2002.01044.x

Campos-Filho EM, Da Costa JNMN, De Sousa OL, Junqueira RGP (2013) Mechanized direct-seeding of native forests in Xingu, central Brazil. J Sustain For 32(7):702–727. https://doi.org/10.1080/10549811.2013.817341

Castro J, Morales-Rueda F, Navarro FB, Löf M, Vacchiano G, Alcaraz-Segura D (2021) Precision restoration: a necessary approach to foster forest recovery in the 21st century. Restor Ecol 29(7):e13421. https://doi.org/10.1111/rec.13421

Castro J, Pérez-García M, Lovenstein H, Pedrini S (2026) Seeding pines in the Mediterranean region. Reforesta 21: 10-31. https://dx.doi.org/10.21750/REFOR.21.02.132

Ceccon E, González EJ, Martorell C (2016) Is direct seeding a biologically viable strategy for restoring forest ecosystems? Evidences from a meta-analysis. Land Degrad Dev 27(3):511–520. https://doi.org/10.1002/ldr.2421

Cole RJ, Holl KD, Keene C, Zahawi RA (2011) Direct seeding of late-successional trees to restore tropical montane forest. For Ecol Manag 261(10):1590–1597. https://doi.org/10.1016/j.foreco.2010.06.038

de Souza DC (2022) Forest restoration by direct seeding: a global bibliometric analysis. Restor Ecol 30(8):e13631. https://doi.org/10.1111/rec.13631

de Souza DC, Engel VL (2018) Direct seeding reduces costs, but it is not promising for restoring tropical seasonal forests. Ecol Eng 116:35–44. https://doi.org/10.1016/j.ecoleng.2018.02.019

de Souza DC, Engel VL (2023) Advances, challenges, and directions for ecological restoration by direct seeding of trees: Lessons from Brazil. Biol Conservation 284:110172. https://doi.org/10.1016/j.biocon.2023.110172

Dias Laumann P, Cardoso Ferreira M, Alves da Silva D, Luis Mascia Vieira D (2023) Germination traits explain the success of direct seeding restoration in the seasonal tropics of Brazil. For Ecol Manag 529:120706. https://doi.org/10.1016/j.foreco.2022.120706

Doust SJ, Erskine PD, Lamb D (2006) Direct seeding to restore rainforest species: Microsite effects on the early establishment and growth of rainforest tree seedlings on degraded land in the wet tropics of Australia. For Ecol Manag 234(1):333–343. https://doi.org/10.1016/j.foreco.2006.07.014

Downer R, Manteuffel-Ross T, Tymon L, Aghai M (2024). Direct seeding for conifer regeneration in the Pacific Northwest: a past, present, and future of operational practices. J For 122(2):171–184. https://doi.org/10.1093/jofore/fvad050

Egerer MH, Fricke EC, Rogers HS (2018) Seed dispersal as an ecosystem service: frugivore loss leads to decline of a socially valued plant, *Capsicum frutescens*. Ecol Appl 28(3):655–667. https://doi.org/10.1002/eap.1667

Elliott S, Blakesley D, Hardwick K (2013) Restoring Tropical Forests: A Practical Guide. Kew Publishing, Kew, UK.

Elliott S, Tucker NI, Shannon DP, Tiansawat P (2023) The framework species method: harnessing natural regeneration to restore tropical forest ecosystems. Philos Trans Royal Soc B 378(1867):20210073. https://doi.org/10.1098/rstb.2021.0073

Engel VL, de Souza DC, Parrotta J (2026) An overview of seeding methods to restore tropical forests of Brasil. Reforesta 21:105-145. https://dx.doi.org/10.21750/REFOR.21.07.137

Fischer H, Huth F, Hagemann U, Wagner S (2015) Developing restoration strategies for temperate forests using natural regeneration processes. In: Stanturf JA (ed) Restoration of Boreal and Temperate Forests, Second Edition, CRC Press, Boca Raton, FL, USA, pp 103–164.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK (2005) Global consequences of land use. Science 309(5734):570–574. https://doi.org/10.1126/science.1111772

Freitas MG, Rodrigues SB, Campos-Filho EM, do Carmo GHP, da Veiga JM, Junqueira RGP, Vieira DLM (2019) Evaluating the success of direct seeding for tropical forest restoration over ten years. For Ecol Manag 438:224–232. https://doi.org/10.1016/j.foreco.2019.02.024

Frischie S, Miller AL, Pedrini S, Kildisheva OA (2020) Ensuring seed quality in ecological restoration: Native seed cleaning and testing. Restor Ecol 28(S3):S239–S248. https://doi.org/10.1111/rec.13217

García D, Zamora R, Hódar JA, Gómez JM, Castro J (2000). Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. Biol Conservation 95(1):31–38. https://doi.org/10.1016/S0006-3207(00)00016-1

Garcia-Orth X, Martínez-Ramos M (2008) Seed dynamics of early and late successional tree species in tropical abandoned pastures: seed burial as a way of evading predation. Restor Ecol 16(3):435–443. https://doi.org/10.1111/j.1526-100X.2007.00320.x

Gardiner E, Stanturf J (2026) Seeding bottomland oaks (*Quercus* spp.) in the southern United States. Reforesta 21: 166-189. https://dx.doi.org/10.21750/REFOR.21.09.139

Gardiner ES, Oliver JM (2005) Restoration of bottomland hardwood forests in the Lower Mississippi Alluvial Valley, USA. In: Stanturf JA, Madsen P (eds) Restoration of Boreal and Temperate Forests. CRC Press, Boca Raton, FL, USA. pp 235–251.

Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D, 2017. Oaks and people: a long journey together. In: Gil-Pelegrín E, Peguero-Pina J, Sancho-Knapik D (eds) Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L. Springer, Cham, Switzerland pp 1–11. https://doi.org/10.1007/978-3-319-69099-5_1

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E (2004) Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. Ecol Appl 14(4):1128–1138. https://doi.org/10.1890/03-5084

Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RT, Sperry JS, McDowell NG (2020) Plant responses to rising vapor pressure deficit. New Phytol 226(6):1550–1566. https://doi.org/10.1111/nph.16485

Grossnickle SC, Ivetić V (2017) Direct seeding in reforestation–a field performance review. Reforesta 4:94–142. https://doi.org/10.21750/REFOR.4.07.46

Grubb PJ (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52(1):107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Guariguata MR (2000) Seed and seedling ecology of tree species in neotropical secondary forests: Management implications. Ecol Appl 10(1):145–154. https://doi.org/10.1890/1051-0761(2000)010[0145:SASEOT]2.0.CO;2

Hankin LE, Leger EA, Bisbing SM (2023) Reforestation of high elevation pines: Direct seeding success depends on seed source and sowing environment. Ecol Appl 33(6):e2897. https://doi.org/10.1002/eap.2897

Ivetić V, Marinković M (2026) Seeding to establish Ravni Srem oak forests, Nothern Serbia. Reforesta 21:199-207. https://dx.doi.org/10.21750/REFOR.21.11.141

Johnston MR, Barnes ML, Preisler Y, Smith WK, Biederman JA, Scott RL, Williams AP, Dannenberg MP (2025) Effects of hot versus dry vapor pressure deficit on ecosystem carbon and water fluxes. J Geophys Res: Biogeosciences 130(1):e2024JG008146. https://doi.org/10.1029/2024JG008146

Kildisheva OA, Dixon KW, Silveira FAO, Chapman T, Di Sacco A, Mondoni A, Turner SR, Cross AT (2020) Dormancy and germination: Making every seed count in restoration. Restor Ecol 28(S3):S256–S265. https://doi.org/10.1111/rec.13140

Laumann PD, Ferreira MC, da Silva DA, Vieira DLM (2023) Germination traits explain the success of direct seeding restoration in the seasonal tropics of Brazil. For Ecol Manag 529:120706.https://doi.org/10.1016/j.foreco.2022.120706

Liu H, Chen Z, Wang Z, Li J (2023) An effective precision afforestation system for UAV. Sustainability 15(3):2212. https://doi.org/10.3390/su15032212

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Tamm Review: Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. For Ecol Manag 448:474–489. https://doi.org/10.1016/j.foreco.2019.06.032

Löf M, Dey DC, Navarro RM, Jacobs DF 2012. Mechanical site preparation for forest restoration. New For 43(5-6):825–848. https://doi.org/10.1007/s11056-012-9332-x

Löf M, Ersson B, Hjältén J, Nordfjell T, Oliet JA, Willoughby I. 2015. Site preparation techniques for forest restoration. In: Stanturf J.A. (ed) Restoration of Boreal and Temperate Forests, Second Edition, CRC Press, Boca Raton, FL, USA, pp 85–102.

Löf M, Miles B, Moe KT, Pohl N, Schönbeck L (2026) Seeding of oak in southern Sweden. Reforesta 21: 190-198. https://dx.doi.org/10.21750/REFOR.21.10.140

López-Barrera F, García-Hernández MÁ (2026) Seeding acorns from montane cloud forest restoration in central Veracruz, Mexico: practical experiences. Reforesta 21:146-165. https://dx.doi.org/10.21750/REFOR.21.08.138

Lord J, Moss-Mason K (2026) Seeding for native afforestation in temperate New Zealand forests. Reforesta 21:68-86. https://dx.doi.org/10.21750/REFOR.21.05.135

Lozano-Baez SE, Morio A, Bonnet B, Valderrama PD, Sánchez OAC, Trujillo JRT, Paladines HM, Flórez M, Gómez E, Medina FJ, Meli P (2025) Lessons learned from direct seeding to restore degraded mountains in Cauca, Colombia. Ecol Manag Restor 26(1):e12625. https://doi.org/10.1111/emr.12625

Madalcho AB, Gazda A, Szwagrzyk J (2025) Ungulate browsing patterns and forage abundance determine the regeneration of palatable tree species: Using new perspectives in assessing ungulate browsing pressure in temperate forests. For Ecosyst 12:100288. https://doi.org/10.1016/j.fecs.2024.100288

Madsen P, Jensen FA, Fodgaard S (2015) Afforestation in Denmark. In: Stanturf J.A. (ed) Restoration of Boreal and Temperate Forests, Second Edition, CRC Press, Boca Raton, FL, USA, pp 201–216.

Madsen P, Löf M (2005) Reforestation in southern Scandinavia using direct seeding of oak (*Quercus robur* L.). Forestry 78(1):55–64. https://doi.org/10.1093/Forestry /cpi005

Merritt DJ, Dixon KW (2011) Restoration seed banks—a matter of scale. Science 332(6028):424–425. https://doi.org/10.1126/science.1203083

Mohan M, Richardson G, Gopan G, Aghai MM, Bajaj S, Galgamuwa GAP, Vastaranta M, Arachchige PSP, Amorós L, Corte APD, de-Miguel S, Leite RV, Kganyago M, Broadbent EN, Doaemo W, Shorab MAB, Cardil A (2021) UAV-supported forest regeneration: Current trends, challenges and implications. Remote Sens 13(13):2596. https://doi.org/10.3390/rs13132596

Naruangsri K, Pathom-aree W, Elliott S, Tiansawat P (2024) Selecting suitable tree species for direct seeding to restore forest ecosystems in northern Thailand. Forests 15(4):674. https://doi.org/10.3390/f15040674

Negreros-Castillo P, Snook LK, Mize CW (2003) Regenerating mahogany (*Swietenia macrophylla*) from seed in Quintana Roo, Mexico: the effects of sowing method and clearing treatment. For Ecol Manag 183(1):351–362. https://doi.org/10.1016/S0378-1127(03)00143-9

Novick KA, Ficklin DL, Grossiord C, Konings AG, Martinez-Vilalta J, Sadok W, Trugman AT, Williams AP, Wright AJ, Abatzoglou JT, Dannenberg MP, Gentine P, Guan K, Johnston MR, Lowman LEL, Moore DJP, McDowell NG (2024) The impacts of rising vapour pressure deficit in natural and managed ecosystems. Plant Cell Environ 47(9):3561–3589. https://doi.org/10.1111/pce.14846

Nunes S, Gastauer M, Cavalcante RBL, Ramos SJ, Caldeira CF, Silva D, Rodrigues R., Salomão R, Oliveira M, Souza-Filho PWM, Siqueira JO (2020). Challenges and opportunities for large-scale reforestation in the Eastern Amazon using native species. For Ecol Manag 466:118120. https://doi.org/10.1016/j.foreco.2020.118120

Oliet JA Jacobs, DF (2012) Restoring forests: advances in techniques and theory. New For 43(5):535–541. https://doi.org/10.1007/s11056-012-9354-4

Oliver CD, Larson BC (1996) Forest Stand Dynamics: Updated Edition. John Wiley and Sons, New York, USA.

Palma AC, Laurance SGW (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Appl Veg Sci 18(4):561–568. https://doi.org/10.1111/avsc.12173

Pansing E, Tomback D (2026) Seeding of whitebark pine (*Pinus albicaulis*) in western north American subalpine forests: Development and application. Reforesta 21:32-53. https://dx.doi.org/10.21750/REFOR.21.03.133

Pedrini S, Balestrazzi A, Madsen MD, Bhalsing K Hardegree, SP, Dixon KW, Kildisheva OA (2020a) Seed enhancement: getting seeds restoration-ready. Restor Ecol 28(S3):S266–S275. https://doi.org/10.1111/rec.13184

Pedrini S, Dixon KW (2020) International principles and standards for native seeds in ecological restoration. Restor Ecol 28(S3):S286–S303. https://doi.org/10.1111/rec.13155

Pedrini S, Gibson-Roy P, Trivedi C, Gálvez-Ramírez C, Hardwick K, Shaw N, Frischie S, Laverack G, Dixon K (2020b) Collection and production of native seeds for ecological restoration. Restor Ecol 28(S3):S228–S238. https://doi.org/10.1111/rec.13190

Piotrowski I, Paladines HM, de Almeida LS, López AMT, Dutra FB, Francisco BS, da Silva JMS, Piña-Rodrigues FCM (2023) Seeds' early traits as predictors of performance in direct seeding restoration. Forests 14(3):547. https://doi.org/10.3390/f14030547

Saldarriaga MG, Lee M, Farquhar S (2025) Does drone-facilitated revegetation work? A case study from Taiwan. Acad Environ Sci Sustain 2:2. https://www.doi.org/10.20935/AcadEnvSci7624

Schmidt L (2008) A review of direct sowing versus planting in tropical afforestation and land rehabilitation. Development and Environment Series 10-2008. Forest & Landscape Denmark, Hørsholm, Denmark.

Schmidt L (2016) Forest seed collection, processing, and testing. In: Pancel L, Köhl M (eds) Tropical Forestry Handbook, Second Edition, Springer, Berlin, Germany. pp 959–994.

Shaw N, Barak RS, Campbell RE, Kirmer A, Pedrini S, Dixon K, Frischie S (2020) Seed use in the field: delivering seeds for restoration success. Restor Ecol 28(S3):S276–S285. https://doi.org/10.1111/rec.13210

Sikström U, Hjelm K, Hanssen K, Saksa T, Wallertz K (2020) Influence of mechanical site preparation on regeneration success of planted conifers in clearcuts in Fennoscandia – a review. Silva Fennica 54(2):10172. https://doi.org/10.14214/sf.10172

Stamatopoulos I, Le TC, Daver F (2024) UAV-assisted seeding and monitoring of reforestation sites: a review. Aust For 87(2):90–98. https://doi.org/10.1080/00049158.2024.2343516

Stanturf JA, Callaham M, e*ds.* (2021) Soils and Landscape Restoration. Academic Press, London, UK.

Stanturf JA, Dumroese RK, Elliott S, Ivetic V, Kleine M, Lang M, Löf M, Madsen P, Prescott C, Khokthong W, Young T (2024). Advances in forest restoration management and technology. In: Katila P, Pierce Colfer CJ, de Jong W, Galloway G, Pacheco P, Winkel G (eds) Restoring Forests and Trees for Sustainable Development: Policies, Practices, Impacts, and Ways Forward. Oxford University Press, Oxford, UK. pp 297–334.

Stanturf JA, Schweitzer CJ, Gardiner ES (1998) Afforestation of marginal agricultural land in the Lower Mississippi River Alluvial Valley, USA. Silva Fennica 32(3):281–297.

Stavi I, Bebre I, Dimitrova A, Stanturf J (2024) Cover cropping to prepare degraded lands for forestry: Challenges and opportunities. New For 55(5):1049–1063. https://doi/org/10.1007/s11056-023-10023-9

Stavi I, Siad SM, Kyriazopoulos AP, Halbac-Cotoara-Zamfir R (2020) Water runoff harvesting systems for restoration of degraded rangelands: A review of challenges and opportunities. J Environ Manag 255:109823. https://doi.org/10.1016/j.jenvman.2019.109823

Sudrajat D, Yulianti, Rustam E (2026) Seeding of tropical tree species in Indonesia. Reforesta 21: 87-104. https://dx.doi.org/10.21750/REFOR.21.06.136

Tanner KE, Parker IM, Fountain MC, Thomsen AS, Wasson K (2025) Unfriendly neighbors: When facilitation does not contribute to restoration success in tidal marsh. Ecol Appl 35(1):e3079. https://doi.org/10.1002/eap.3079

Tiansawat P, Elliott S (2020) Unmanned aerial vehicles for automated forest restoration. In: Elliott S, Gale G, Robertson M (eds.) Automated forest restoration: Could robots revive rain forests? Proceedings of a brain-storming workshop, FORRU-CMU, Chiang Mai University, Chiang Mai, Thailand, pp 28–45.

Toumey JW (1916) Seeding and Planting. John Wiley and Sons, New York, USA.

Tunjai P (2012) Direct Seeding for Restoring Tropical Lowland Forest Ecosystems in Southern Thailand. PhD Thesis, Walailak University, Thasala District Nakhonsrithammarat, Thailand. 216 pp.

Tunjai P, Elliott S (2012) Effects of seed traits on the success of direct seeding for restoring southern Thailand's lowland evergreen forest ecosystem. New For 43:319–333. https://doi.org/10.1007/s11056-011-9283-7

Vallejo VR, Smanis A, Chirino E, Fuentes D, Valdecantos A, Vilagrosa A (2012) Perspectives in dryland restoration: approaches for climate change adaptation. New For 43(5-6):561–579. https://doi.org/10.1007/s11056-012-9325-9

Vieira DLM, de Lima VV, Sevilha AC, Scariot A (2008). Consequences of dry-season seed dispersal on seedling establishment of dry forest trees: Should we store seeds until the rains? For Ecol Manag 256(3):471–481. https://doi.org/10.1016/j.foreco.2008.04.052

Vozzo JA, ed (2002) Tropical Tree Seed Manual. US Department of Agriculture, Forest Service, Agriculture Handbook 721. Washinton, DC, USA.

Waiboonya P, Elliott S (2020) Sowing time and direct seeding success of native tree species for restoring tropical forest ecosystems in northern Thailand. New For 51(1):81–99. https://doi.org/10.1007/s11056-019-09720-1

Wang FC, Liu Q, Wang GG (2026) *Pinus massoniana* seeding practices for forest restoration in China. Reforesta 21:54-68. https://dx.doi.org/10.21750/REFOR.21.04.134

Willoughby I, Jinks RL (2009) The effect of duration of vegetation management on broadleaved woodland creation by direct seeding. Forestry 82(3):343–359. https://doi.org/10.1093/*Forestry* /cpp012

Willoughby I, Jinks RL, Kerr G, Gosling PG (2004) Factors affecting the success of direct seeding for lowland afforestation in the UK. Forestry 77(5):467–482. https://doi.org/10.1093/Forestry /77.5.467

Willoughby IH, Jinks RL, Forster J (2019) Direct seeding of birch, rowan and alder can be a viable technique for the restoration of upland native woodland in the UK. Forestry 92(3):324–338. https://doi.org/10.1093/Forestry/cpz018

Witzell J, Oliet JA, Vilagrosa A, Kanjevac B, Hanssen KH, Chiatante D, Bebre I, Madsen P, Çerçioğlu M (2026) Forward-looking practices for climate-responsive site preparation, direct seeding, and planting. In: Stanturf JA, Villar-Salvador P, Mariotti B, Ivetić V, Madsen P, Montagnoli A, Andivia E, Bebre I, Dimitrova A, Klisz M (eds) Guidelines for Climate Adaptive Forest Restoration and Reforestation Projects, Elsevier. pp. 193-241. https://doi.org/10.1016/B978-0-443-34086-4.00010-4

Woods K, Elliott S (2004) Direct seeding for forest restoration on abandoned agricultural land in northern Thailand. J Trop For Sci 16:248–259.