



## Seeding forest trees

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### ARTICLE INFO

#### Citation:

Stanturf J, Gardiner E (2026)  
Seeding forest trees. *Reforesta* 21:  
208-224.

DOI: <https://dx.doi.org/10.21750/REFOR.21.12.142>

**Editor:** Vladan Ivetić

**Received:** 15.11.2025

**Accepted:** 15.12.2025

**Published:** 20.01.2026



#### Note

This paper is a part of Special issue on International Practices for Regenerating and Restoring Forest Trees by Seeding, edited by Emile S Gardiner and John A Stanturf

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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

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## 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. (Löff 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<sup>-1</sup>) 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<sup>-1</sup> 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 (Löff et al. 2012; Löff 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 (Löff 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<sup>-1</sup> for species planted in rows. Higher rates are suggested for broadcasting, ranging from 12,500-37,500 seeds ha<sup>-1</sup> (Grossnickle and Ivetić 2017) although even higher rates, from

100,000 to 500,000 seeds ha<sup>-1</sup>, 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.

## 9 Acknowledgement

The article is an activity within the work of IUFRO Task Force “Transforming Forest Landscapes for Future Climates and Human Well-Being.” We thank the editors and two anonymous reviewers for helpful suggestions.

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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.

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