



# 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

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## 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<sup>2</sup> territory (Oliveira et al. 2022), currently covering about 58% of the total land area (MapBiomias 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 (MapBiomias 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 (MapBiomias 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% (MapBiomias 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 (MapBiomias 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 16<sup>th</sup> 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).

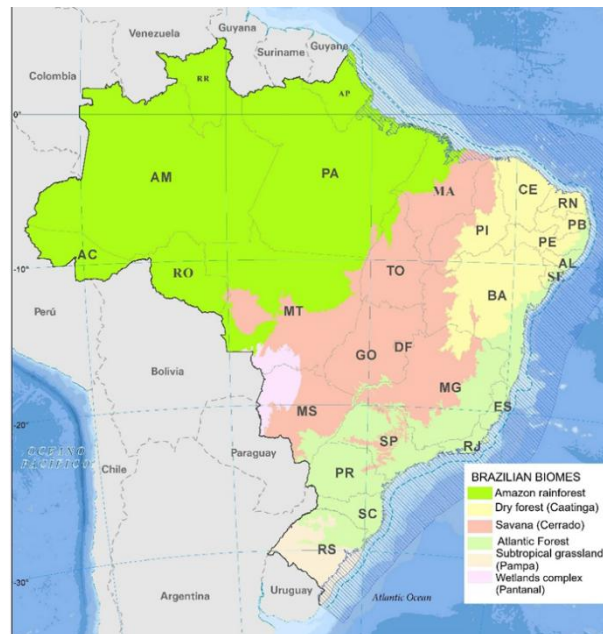


Figure 1. Major Brazilian terrestrial biomes according to IBGE classification. Forests and woodlands are found in all biomes. Two-letter abbreviations denote Brazilian state names. Adapted from IBGE (2024).

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 (MapBiomias 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).

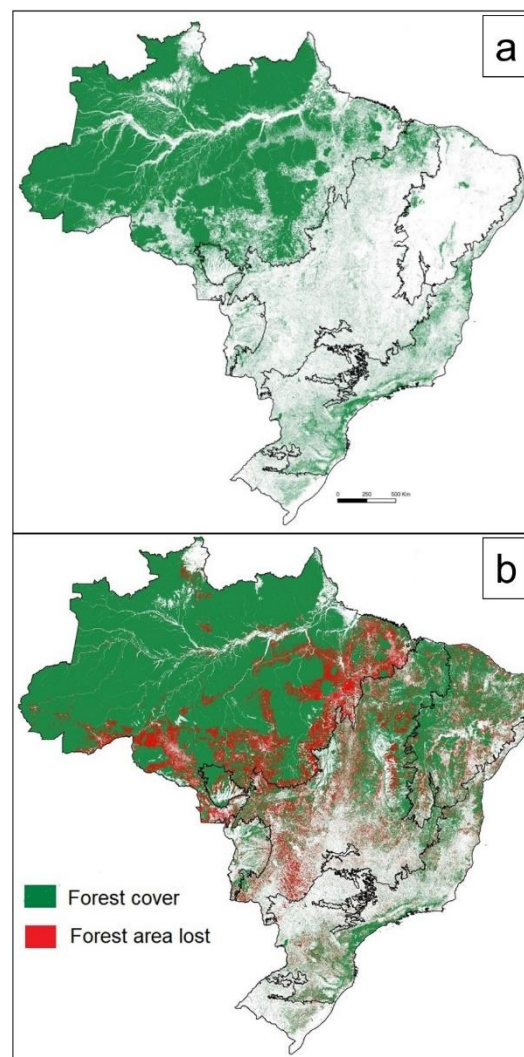


Figure 2. (a) Current forest cover in Brazil (including savanna and dry forest woodlands). (b) Loss of forest cover from 1985 to 2022. Adapted from MapBiomias (2023).

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 et 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).

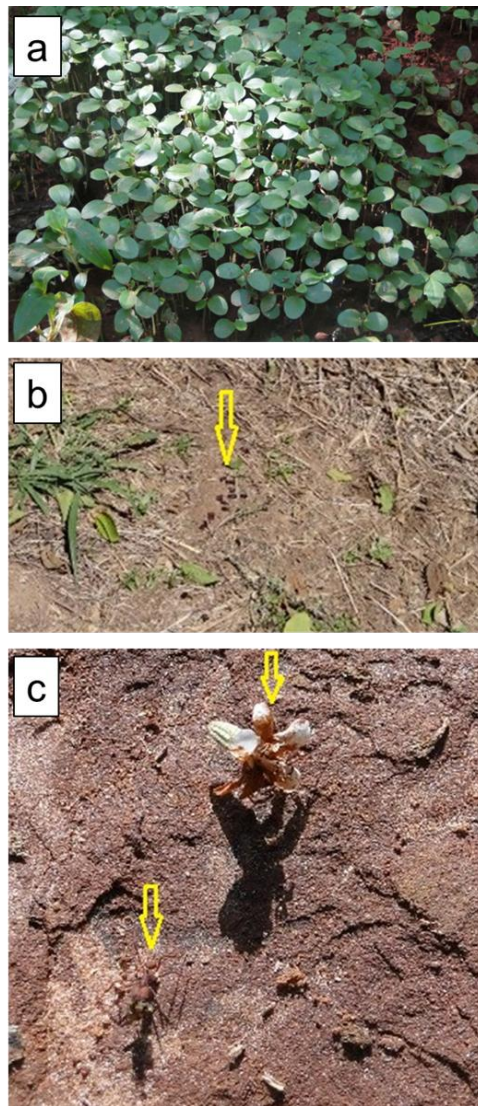


Figure 3. Effects of leaf-cutting ants (*Atta* spp. Fabricius) at restoration sites. (a) Seedlings of *Croton floribundus* Spreng. (Euphorbiaceae), a common species used in restoration plantings in the Atlantic Forest, which have germinated over an ant nest. (b) Seeds of *Anadenanthera colubrina* var. *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<sup>-1</sup>; 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., *Megathyrus* spp., *Melinis* 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., Haloxypop-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<sup>-1</sup> 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<sup>-1</sup>) 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 (Brançalion 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 aculeata* (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.caminhosdamente.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 (Laumann 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, *Dypteryx 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. *corrugata* 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<sup>-2</sup>) or high density (65 seed m<sup>-2</sup>) (NEMA/UNIVASF 2023).

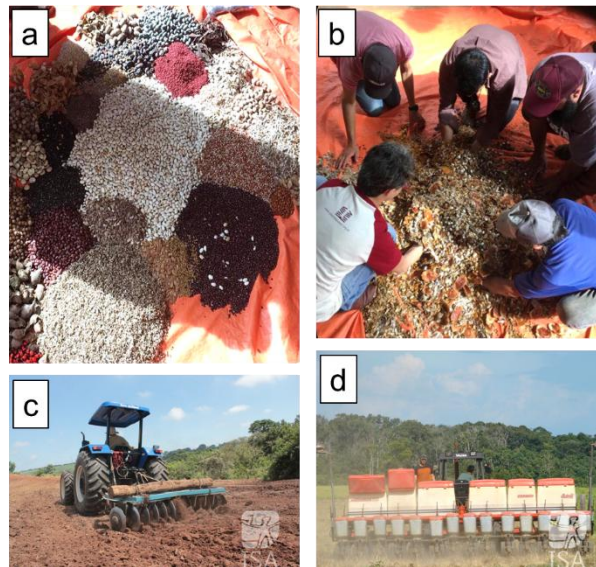


Figure 5. (a) and (b) Preparation of “muvuca” seed mixes for sowing. (c) Harrowing to incorporate sown seed into soil after broadcast sowing. (d) Mechanized broadcast “muvuca” seeding with a soybean (*Glycine max* (L.) Merr.) planter. (Photo credits: (a, b) R.B.G. da Silva; (c, d) by ISA, <https://acervo.socioambiental.org/>).



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<sup>-1</sup>) (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<sup>-1</sup>, respectively) while mechanically line sowing with minimum cultivation.

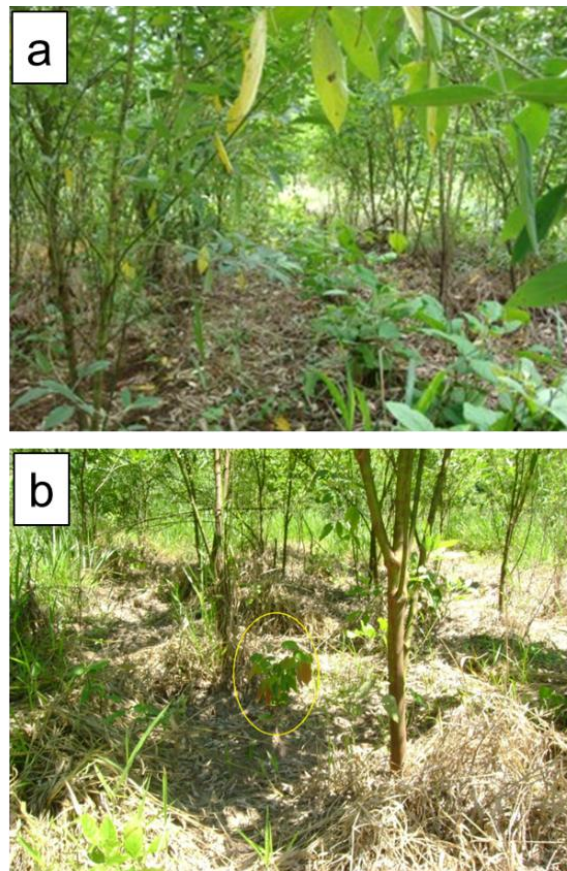


Figure 7. Beneficial effect of green manure plants established with seeded tree species. (a) The quick-forming canopy of pigeon pea (*Cajanus cajan* (L.) Huth) that was sown in alternating lines with tree species. (b) A seedling of a climax species, *Hymenaea courbaril* L. (Fabaceae), under the shade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

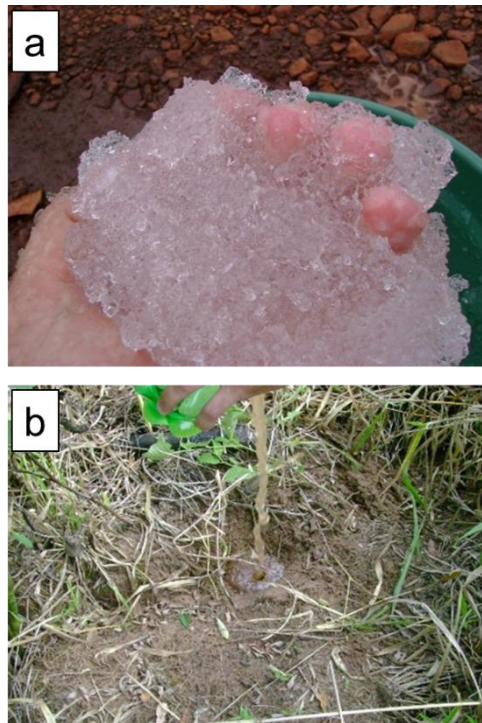


Figure 8. Hydrogel amendment during sowing. (a) Hydrogel solution prepared for application; (b) hydrogel application into the seeding hole. (Photo credits: D.C. de Souza).

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<sup>-1</sup> 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<sup>-1</sup> for line seeding, and 203,850 seed ha<sup>-1</sup> 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<sup>-1</sup>, and about 20% sowed more than 500,000 seed ha<sup>-1</sup> (Souza and Engel 2023). Sowing rates of 145,000 to 1,666,000 seed ha<sup>-1</sup> 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<sup>-2</sup> muvuca mix corresponded to 200,000 to 400,000 seed ha<sup>-1</sup>. For the Cerrado-Amazon transition, more than 286,000 seed ha<sup>-1</sup> are recommended for broadcast or line seeding and 214,000 seed ha<sup>-1</sup> for seeding of seeding holes (Vieira et al. 2020). For Caatinga Dry Forests, sowing rate can surpass 1,000,000 seed ha<sup>-1</sup> when mechanical broadcast seeding (360,000 seed ha<sup>-1</sup> of the cover species *Senna uniflora* (Mill.) H.S. Irwin & Barneby combined with 650,000 seed ha<sup>-1</sup> 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<sup>-1</sup> 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 *Megathyrus* 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  $\text{ha}^{-1}$  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; Sukanuma 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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**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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