

Biology-Botany

Imbibition patterns in native seeds: insights for direct seeding in restoration ecology

Padrões de embebição em sementes nativas: insights para semeadura direta na ecologia da restauração

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ABSTRACT

Seed imbibition directly influences germination and seedling establishment, playing a crucial role in optimizing germination protocols and enhancing seed use in restoration projects. This study aimed to characterize the imbibition patterns and germination dynamics of eleven native forest species commonly used in direct seeding. Imbibition curves were analyzed using four replicates of 25 seeds per species, placed in paper rolls moistened with distilled water (2.5 times their mass) and incubated in BOD chambers at 25°C or 30°C, depending on the species. Seeds were weighed at two-hour intervals during the first 12 hours and then every 24 hours until primary root protrusion (≥ 2 mm) occurred. All species followed a triphasic water absorption model, with substantial variation in the duration of the phases. Phase I ranged from 2 to 24 hours, Phase II lasted between 12 and 144 hours, and Phase III occurred within 24 to 168 hours, depending on the species. Rapid radicle protrusion was observed in *Mimosa bimucronata* (DC.) Kuntze and *Senegalia polyphylla* (DC.) Britton & Rose (24 hours), while *Handroanthus impetiginosus* (Mart. ex DC.) Mattos and *Maclura tinctoria* (L.) D. Don ex Steud. exhibited prolonged germination times (168 hours). These results highlight the diversity in imbibition dynamics among species and provide critical insights into their potential application in direct seeding. Understanding such patterns is essential for selecting species and designing protocols to improve the success of ecological restoration initiatives.

Keywords: Water absorption; Germination pattern; Imbibition curve

RESUMO

A embebição de sementes influencia diretamente a germinação e o estabelecimento de plântulas, desempenhando um papel crucial na otimização de protocolos de germinação e no aumento do uso de sementes em projetos de restauração. Este estudo teve como objetivo caracterizar os padrões de embebição e a dinâmica de germinação de onze espécies florestais nativas comumente usadas em semeadura direta. As curvas de embebição foram analisadas usando quatro réplicas de 25 sementes por espécie, colocadas em rolos de papel Germitest® umedecidos com água destilada (2,5 vezes sua massa) e incubadas em câmaras BOD a 25 °C ou 30 °C, dependendo da espécie. As sementes foram pesadas em intervalos de duas horas durante as primeiras 12 horas e depois a cada 24 horas até que ocorresse a protrusão da raiz primária (≥ 2 mm). Todas as espécies seguiram um modelo trifásico de absorção de água, com variação substancial na duração das fases. A Fase I variou de 2 a 24 horas, a Fase II durou entre 12 e 144 horas, e a Fase III ocorreu dentro de 24 a 168 horas, dependendo da espécie. Protrusão rápida da radícula foi observada em *Mimosa bimucronata* (DC.) Kuntze e *Senegalia polyphylla* (DC.) Britton & Rose (24 horas), enquanto *Handroanthus impetiginosus* (Mart. ex DC.) Mattos e *Maclura tinctoria* (L.) D. Don ex Steud. exibiram tempos de germinação prolongados (168 horas). Esses resultados destacam a diversidade na dinâmica de embebição entre as espécies e ressaltam pontos chave para sua aplicação potencial na semeadura direta. Entender esses padrões é essencial para selecionar espécies e projetar protocolos para melhorar o sucesso de iniciativas de restauração ecológica.

Palavras-chave: Absorção de água; Padrão germinativo; Curva de embebição

1 INTRODUCTION

Seed germination is a critical phase in the plant life cycle, as it determines the successful establishment of seedlings. This process is influenced by factors such as physiological maturity, water content, and reserve composition, which vary among species. When exposed to an appropriate substrate and favorable environmental conditions, seeds resume metabolic activities and initiate embryo development (Carvalho & Nakagawa, 2012; Pereira et al., 2022; Nautiyal et al., 2023). Germination begins with water imbibition, during which the seed absorbs water, consumes stored reserves, and prepares for primary root protrusion, marking the transition to nutrient uptake from the environment (Schmidt, 2007; Borges & Toorop, 2015; Aumonde et al., 2019).

Imbibition follows a triphasic model of water absorption, with each phase characterized by distinct physiological and biochemical changes. Phase I (PI) involves rapid water uptake due to the dry seed's matrix potential, resulting in increased seed

mass and initial metabolic activation (Bewley & Black, 1994; Cardoso, 2013; Taiz et al., 2017). Phase II (PII) is marked by a stabilization of water content, with seeds maintaining a constant or slightly increased mass as metabolic processes are activated and cellular structures repaired. Finally, Phase III (PIII) is characterized by a renewed increase in water absorption associated with embryo growth, culminating in the protrusion of the primary root (Castro & Hilhorst, 2004; Cardoso, 2013; Taiz et al., 2017).

The duration and dynamics of the imbibition process vary among species, influenced by seed morphology, chemical composition, and tegument permeability. The seed coat plays a crucial role during imbibition by regulating water entry and acting as a reservoir in the early stages of germination (Silva & Dantas, 2016). Seeds with high oil content, for example, tend to absorb less water compared to starchy or protein-rich seeds, leading to differences in absorption speed and intensity (Bewley et al., 2013). Additionally, factors such as tegument porosity, structure, and pigmentation influence water permeability and hydration efficiency (Marcos-Filho, 2015; Ribeiro- Oliveira & Silva, 2024).

Laboratory germination tests provide valuable insights into the germination potential of seeds under controlled conditions. These tests allow for the evaluation of seed quality and vigor, facilitating comparisons of physiological potential, determining germination rates for sowing and commercial use, and identifying optimal storage conditions (Carvalho & Nakagawa, 2012). Understanding imbibition periods is particularly important, as this phase governs key processes such as tegument permeability, reserve mobilization, and the onset of metabolic activity (Borges et al., 2002).

Monitoring imbibition patterns is essential for optimizing seed germination and maximizing seedling emergence under field conditions. A precise understanding of water uptake dynamics allows for better prediction of germination timing and facilitates the development of species-specific pre-sowing treatments to enhance performance in restoration scenarios (Finch-Savage & Bassel, 2016); Nautiyal et al., 2023).

Moreover, characterizing the imbibition behavior of native forest species used in ecological restoration offers key insights into their functional responses under direct seeding conditions. This is particularly relevant for species with contrasting ecological strategies and functional traits, as variations in seed coat permeability, reserve composition, and dormancy mechanisms can strongly influence germination success and field establishment (Rajjou et al., 2012; Bewley et al., 2013). By integrating these physiological parameters into species selection and sowing strategies, restoration practitioners can design more effective, context-specific interventions to accelerate ecosystem recovery in degraded landscapes.

Variations among the duration of the three imbibition phases (PI, PII, and PIII) can reflect species-specific adaptations that can be quantified under controlled conditions. Understanding these differences provides insights into the germination potential of these species, supporting their optimized use in direct seeding for ecological restoration. Thus, this study aims to characterize the imbibition patterns and germination dynamics of native forest species used in direct seeding to identify and compare variations in the duration of the imbibition phases (PI, PII, and PIII) across species.

2 MATERIAL AND METHODS

Species were selected for direct seeding based on the criteria proposed by Piotrowski et al. (2023), which emphasize small and/or lightweight seeds from different successional groups that exhibit high germination rates under laboratory conditions (>30%) but low emergence and establishment in the field. The selected species included representatives from the families Fabaceae (*Mimosa bimucronata* [DC.] Kuntze, *Senegalia polyphylla* [DC.] Britton & Rose, *Pterogyne nitens* Tul., *Poecilanthe parviflora* Benth), Malvaceae (*Apeiba tibourbou* Aubl., *Ceiba speciosa* [A.St.-Hil.] Ravenna, *Guazuma ulmifolia* Lam.), Bixaceae (*Bixa orellana* L.), Anacardiaceae (*Astronium*

urundeuva [M.Allemão] Engl.), Bignoniaceae (*Handroanthus impetiginosus* [Mart. ex DC.] Mattos), and Moraceae (*Maclura tinctoria* [L.] D.Don ex Steud.).

Seeds were obtained from commercial suppliers between August and December 2023 to ensure a diversity of provenances and a representative mix of maternal genotypes. Analyses were carried out between October and December 2023, with seeds stored at 5°C in a cold chamber until the beginning of the experiments. Seed lots were characterized for moisture content using the oven-drying method (105°C for 24 hours), thousand seed weight (TSW), and the number of seeds per kilogram, in accordance with Brazilian seed testing regulations (Brazil, 2009) (Table 1). The seeds of *A. urundeuva* and *G. ulmifolia* had their dormancy overcome by soaking the seeds in water for 48 hours, followed by immersion at 90°C and water soak for 1 hour off the heat, as recommended by the Guidelines for Forest Seed Analysis (Brazil, 2013).

Table 1 – Physical characterization of seed species based on seed moisture content, thousand seed weight (TSW), and seed count per kilogram

Species	Water content (%)	TSW (g)	Nº seeds/kg
<i>Mimosa bimucronata</i> (DC.) Kuntze	10.17	8.60	116.278
<i>Senegalia polyphylla</i> (DC.) Britton & Rose	8.79	101.85	9.818
<i>Ceiba speciosa</i> (A.St.-Hil.) Ravenna	21.27	164.88	6.065
<i>Guazuma ulmifolia</i> Lam.	8.58	6.59	151.570
<i>Pterogyne nitens</i> Tul.	11.49	131.57	7.601
<i>Bixa orellana</i> L.	14.45	12.54	79.714
<i>Apeiba tibourbou</i> Aubl.	8.47	4.18	239.103
<i>Astronium urundeuva</i> (M.Allemão) Engl.	14.43	14.11	70.874
<i>Poencilanthe parviflora</i> Bentham	14.35	305.20	3.277
<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	13.36	150.87	6.628
<i>Maclura tinctoria</i> (L.) D.Don ex Steud.	9.48	4.01	248.694

Source: Authors (2024)

Four replicates of 25 seeds were used to evaluate the imbibition process. The seeds were placed on germination paper, arranged in roll form, and moistened with distilled water at 2.5 times their dry weight. The paper rolls were enclosed in plastic bags to maintain humidity and incubated in a *Biochemical Oxygen Demand* (BOD)

germinator under a 12-hour photoperiod at 25°C, except for *Mimosa bimucronata* and *Apeiba tibourbou*, which were maintained at 30°C. Seeds were weighed at two-hour intervals during the first 12 hours of imbibition and then every 24 hours thereafter. Monitoring continued until germination stabilized, defined as the protrusion of the primary root to a length of ≥ 2 mm.

The imbibition curves were generated based on the increase in seed water content (%) over time, modeled using a third-order polynomial equation: $A+BX+CX^2+DX^3$. This model was selected due to its close resemblance to a sigmoidal curve, as determined by the relationship between water content percentage and imbibition duration. Data analysis was conducted using R software version 4.2.2 (R Core Team, 2022).

3 RESULTS AND DISCUSSION

Imbibition monitoring revealed that all species followed the three-phase water absorption model proposed by Bewley & Black (1994) (Figure 1). However, significant differences were observed in the duration of each phase. Phase I (PI), the initial rapid water uptake, varied among species, lasting from 2 to 16 hours, as also described by Marcos-Filho (2015). Specifically, PI was completed within 2 hours for *Guazuma ulmifolia* and *Senegalia polyphylla*, 4 hours for *Apeiba tibourbou*, 6 hours for *Astronium urundeuva* and *Mimosa bimucronata*, 8 hours for *Ceiba speciosa* and *Pterogyne nitens*, 12 hours for *Bixa orellana*, *Handroanthus impetiginosus*, and *Poecilanthe parviflora*, and up to 24 hours for *Maclura tinctoria*.

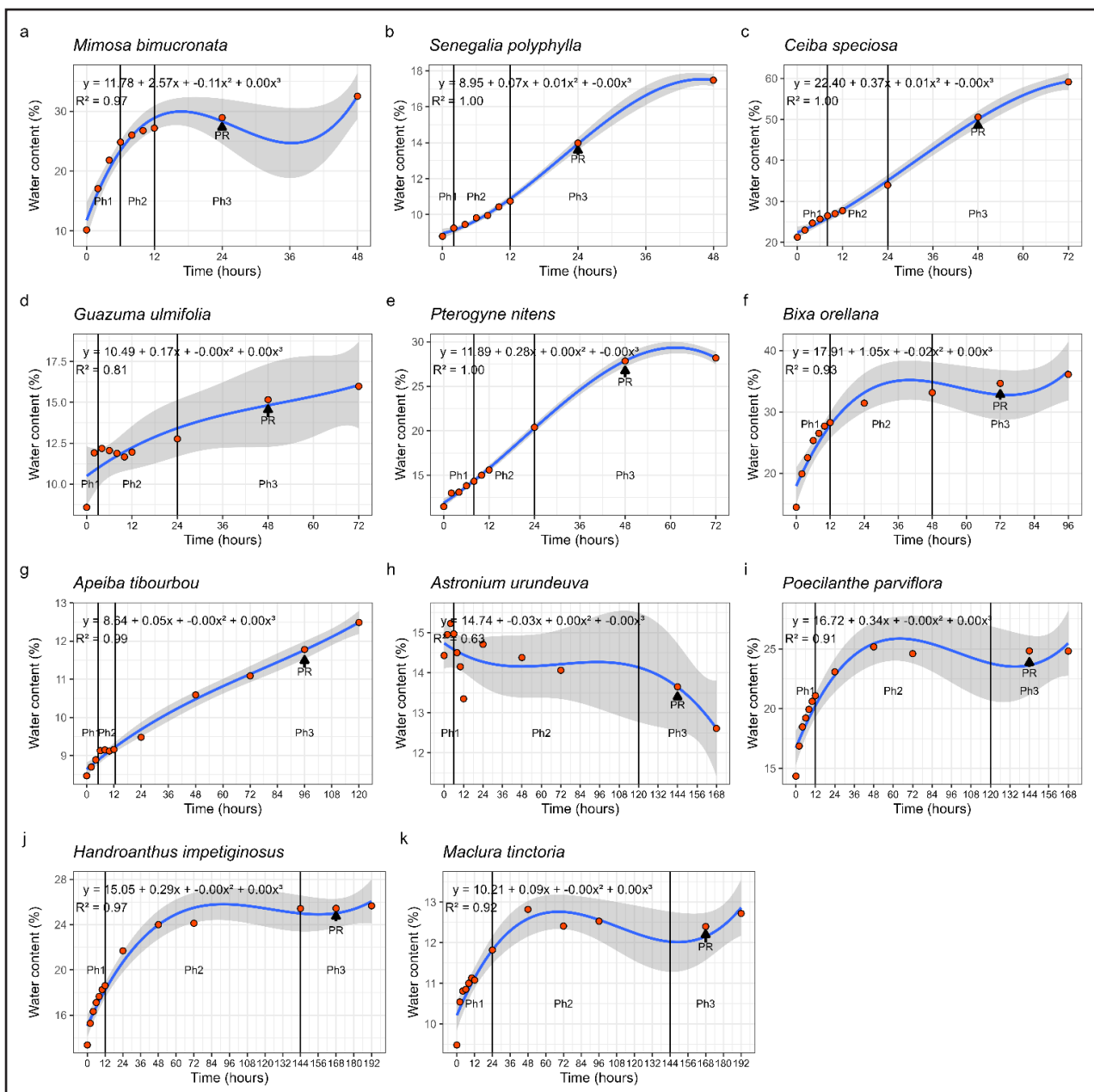
Phase II (PII), characterized by a plateau in water uptake, showed substantial interspecific variation, ranging from 12 hours in *A. tibourbou*, *M. bimucronata*, and *S. polyphylla* to 144 hours in *M. tinctoria* and *H. impetiginosus*. While the extended duration of PII in some species may be partly attributed to the activation of DNA and membrane repair mechanisms during early germination, particularly in seeds subjected to prolonged storage (Rajjou & Debeaujon, 2008; El-Maarouf-Bouteau & Bailly, 2008), we hypothesize that this variation is also strongly influenced by functional seed traits.

These traits may include seed coat characteristics such as thickness, permeability, and mechanical resistance, which directly influence the rate and uniformity of water uptake (Upreti et al., 2024; Zhou et al., 2022). Additionally, the chemical composition of seeds—particularly the type and abundance of storage reserves (proteins, lipids, and carbohydrates) and antioxidant metabolites—affects both hydration dynamics and the speed of metabolic reactivation (Ali & Elozeiri, 2017; Soriano et al., 2013). Together, these structural and biochemical traits contribute to species-specific imbibition behaviors and may be key determinants of germination performance under field conditions.

The autoecology of each species, including adaptations to specific environmental conditions, may influence the duration of PII by modulating seed dormancy and germination strategies (Fenner & Thompson, 2005). As proposed by these authors, species with harder seed coats or higher lipid content may exhibit prolonged PII due to slower water absorption or delayed metabolic processes (Bewley et al., 2013; Baskin & Baskin, 2014). Similarly, species from habitats with unpredictable moisture availability may have evolved slower germination processes as a bet-hedging strategy to ensure establishment under favorable conditions (Fenner & Thompson, 2005). Further exploration of these traits, combined with a deeper understanding of their ecological significance, could provide valuable insights into the germination patterns observed in this study.

The primary root emission (PIII) occurred most rapidly in *Mimosa bimucronata* and *Senegalia polyphylla* (24 hours; Figure 1-a;b) followed by *Ceiba speciosa*, *Guazuma ulmifolia*, and *Pterogyne nitens* (48 hours; Figure 1-c;d;e). Intermediate durations were observed in *Bixa orellana* (72 hours; Figure 1-f) and *Apeiba tibourbou* (96 hours; Figure 1-g). The most prolonged periods for primary root emergence were recorded for *Astronium urundeuva* and *Poecilanthe parviflora* (144 hours; Figure 1-h;i) and *Handroanthus impetiginosus* and *Maclura tinctoria* (168 hours; Figure 1-j;k).

Figure 1 – Imbibition curves of the 11 studied species. (a) *Mimosa bimucronata* and (b) *Senegalia polyphylla* showed primary root emission at 24 h. (c) *Ceiba speciosa*, (d) *Guazuma ulmifolia*, and (e) *Pterogyne nitens* at 48 h. (f) *Bixa orellana* and (g) *Apeiba tibourbou* at 72–96 h. (h) *Astronium urundeuva* and (i) *Poecilanthe parviflora* at 144 h, and (j) *Handroanthus impetiginosus* and (k) *Maclura tinctoria* at 168 h. The red points represent the increase in water content (%) in the imbibition phases (I, II, III), the blue line indicates the trend, the gray area the confidence interval and the arrow indicates the primary root protrusion (PR)



Source: Authors (2024)

The germination process in seeds, in particular the transition through phases I (PI), II (PII), and III (PIII), reflects complex interactions between the physical properties of the seed and its ecological adaptations. The emission of the primary root (PIII) is a critical milestone, marking the beginning of resource acquisition and seedling establishment. Our findings indicate substantial variation in the duration of these phases among the studied species, highlighting potential adaptive strategies for different ecological contexts and implications for direct seeding.

Species such as *Mimosa bimucronata* and *Senegalia polyphylla*, which complete PIII within 24 hours, exemplify traits advantageous for early establishment in direct seeding projects. Their short PI and PII phases likely reflect efficient water absorption and rapid metabolic activation, reducing the lag time between hydration and germination. This swift response confers significant adaptive advantages, particularly in environments where water availability is transient or unpredictable. Rapid root emergence allows seedlings to establish early access to soil moisture, anchoring the seedling and reducing desiccation risk (Baskin & Baskin, 2014; Finch-Savage & Bassel, 2016).

The biochemical basis for these differences may lie in the composition of hydrophilic compounds, such as soluble carbohydrates and storage proteins, which facilitate faster hydration and metabolic reactivation (Bewley et al., 2013). Additionally, thinner or more permeable seed coats may expedite water uptake, as observed in species like *C. speciosa* and *P. nitens* (Silva & Dantas, 2016).

In contrast, species with prolonged PIII phases, such as *Handroanthus impetiginosus* and *Maclura tinctoria* (168 hours), likely represent bet-hedging strategies suited for less predictable environments. These species may rely on slower imbibition rates or mechanisms to delay germination until environmental conditions are optimal, minimizing the risk of seedling mortality during unfavorable periods (Fenner & Thompson, 2005; Dürr et al., 2015). The extended duration of PII in these species may also reflect higher investment in metabolic repair or the mobilization of stored reserves, enhancing seedling vigor once germination occurs (Masetto et al., 2014).

Imbibition is influenced by functional traits, including seed coat permeability, chemical composition, and storage compound type. For example, species with high lipid content, such as *Bixa orellana*, may exhibit slower water uptake during PI and PII, as lipids require emulsification before metabolism can begin (Bewley & Black, 1994). Additionally, species with thicker seed coats, such as *H. impetiginosus*, may demonstrate extended PII due to the slower rate of water penetration and oxygen diffusion (Silva & Dantas, 2016).

From the literature, variations in PI duration among forest species further support this hypothesis. For instance, rapid PI completion was observed in Bignoniaceae species such as *Jacaranda brasiliana* 2 hours (Lima et al., 2018) and *Handroanthus chrysotrichus* 4 hours (Guollo et al., 2018), while species like *Sapindus saponaria* (Sapindaceae) required 71 hours (Torres et al., 2020). These differences underline the importance of both intrinsic traits and environmental factors in shaping imbibition dynamics.

In direct seeding, combining fast- and slow-germinating species can enhance restoration outcomes by aligning functional traits with ecological roles. Pioneer species such as *M. bimucronata* and *S. polyphylla*, characterized by rapid imbibition and germination, are well-suited for early establishment, soil stabilization, and microsite amelioration. These species can mitigate erosion, improve nutrient cycling, and provide shade, facilitating the recruitment of slower germinating species like *M. tinctoria* and *H. impetiginosus*, which contribute to long-term resilience and diversity (Moles & Westoby, 2004; Finch-Savage & Bassel, 2016). Differences in imbibition dynamics reflect distinct germination strategies shaped by environmental pressures. Rapid imbibing species typically exhibit traits such as small seed size, fast establishment, and tolerance to open, exposed environments. In contrast, slow-imbibing species may rely on more stable moisture conditions and often benefit from facilitation by earlier-establishing species (Saatkamp et al., 2019; Larson & Funk, 2016). Recognizing these physiological and ecological complementarities is crucial for optimizing species mixtures especially in contexts of increasing climatic variability and soil degradation.

A notable gap in the literature exists regarding the imbibition and germination processes of the studied species. Understanding these dynamics at the biochemical and ecological levels is critical for optimizing their use in restoration. Future studies should investigate the molecular pathways that control water uptake, metabolic activation, and stress responses during germination, particularly for species with significant variability in imbibition patterns.

4 CONCLUSIONS

This study revealed significant variation in the duration of the triphasic water absorption model (PI, PII, and PIII). Phase I ranged from 2 to 24 hours, Phase II from 12 to 144 hours, and Phase III from 24 to 168 hours, reflecting species-specific differences in hydration efficiency. These variations underscore the influence of functional seed traits, such as seed coat permeability and reserve composition, on germination dynamics.

The results provide valuable insights into the potential application of these species in ecological restoration. We identified rapid imbibition and germination, such as *Mimosa bimucronata* and *Senegalia polyphylla*, ideal for early establishment, and slower-imbibing species like *Handroanthus impetiginosus* and *Maclura tinctoria*. Understanding these imbibition patterns supports the optimization of direct seeding protocols, enhancing the efficiency and success of restoration efforts while contributing to biodiversity recovery in degraded ecosystems.

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