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Key decision-making criteria for dormancy-breaking and ability to form seed banks of Cerrado native tree species

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ABSTRACT

Ecological restoration by direct seeding in the Cerrado biome still lacks information about native species germination, the need for dormancy overcoming and seed bank formation. This study aims to verify the effects of dormancy overcoming on germination of four tree species and the ability of 12 tree species to form seed banks for restoration use. Our results showed wide variation of species' germination rates. Overcoming dormancy enhanced germination for *Dimorphandra mollis*, *Hymenaea stigonocarpa*, and *Peltophorum dubium* and decreased it for *Copaifera langsdorffii*, but was only cost-effective for *H. stigonocarpa*. Regarding the ability to form seed banks, only *H. stigonocarpa* and *Cecropia pachystachya* germinated and live seedlings of *Terminalia corrugata* were found after being buried for six months, thus forming a transient seed bank. Despite the fact that overcoming dormancy may optimize germination after direct seeding, maintaining dormancy mechanisms of species that can form seed banks could be essential for species establishment over time in restoration areas. Hence, our key decision criteria based on seed costs and seed and labor availability would be useful for the seeding actions of restoration practitioners.

Keywords: direct sowing, ecophysiology, neotropical savanna, restoration ecology, seed photoblastism

Introduction

Major ecological restoration commitments around the world require information about the cost-benefit of techniques and species used for restoration (Aronson *et al.* 2011; Bussato *et al.* 2015). Compared to seedling planting, direct sowing of tree species has proven to be an efficient and inexpensive technique (Camargo *et al.* 2002; Woods & Elliott 2004; Sovu *et al.* 2010; Guerin *et al.* 2015; Ceccon *et al.* 2016). However, to be viable, it is necessary to understand the characteristics of species used in direct seeding such as germination rates, seed dormancy, and seed bank formation (Engel & Parrotta 2001). Characteristics such as timing of seed dispersal and dormancy seem to control germination timing, and recruitment of woody species in strongly seasonal ecosystems as Neotropical Savannas, also known as Cerrado in Brazil (Salazar *et al.* 2011). In the Cerrado, a biome composed of a mosaic of vegetation varying from grasslands to forests, knowledge about dormancy, germination, and seed bank formation of native species is still scarce when compared to other

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Brazilian biomes (Lima *et al.* 2014; Palma & Laurance 2015; Salazar *et al.* 2012a). Information about species biology, *e.g.*, the need to overcome dormancy and the possibility of seed bank formation, is essential for restoration planning and success, as well as for reducing costs (Khurana & Singh 2001; Salazar *et al.* 2012b).

Seed viability loss could further reduce the seed supply of woody plants by preventing the formation of persistent seed banks (seeds living in the soil for over a year) from which seedlings can recruit (Salazar *et al.* 2012a). Dormancy protects seeds from adverse conditions that do not favor species establishment (Finch-Savage & Leubner-Metzger 2006; Venable 2007; Childs *et al.* 2010; Footitt & Finch-Savage 2017), and at the same time is responsible for seed bank formation (Garwood 1989). The seed bank helps reestablish natural populations after disturbances and is an important component of species diversity conservation that is related to environmental resilience (Tres *et al.* 2007; Martins 2008; Bussato *et al.* 2015). Moreover, the seed bank could potentially be used for restoration purposes (Kiss *et al.* 2019) and seed dormancy is critical for that. Introducing species that can tolerate climatic changes through transient seed bank formation could support passive restoration, particularly in more degraded sites (Kiss *et al.* 2018).

In order to guarantee succession, ecological restoration must consider the characteristics of seed germination, the time in which seeds remain viable in soil banks, and the conditions that lead to dormancy breaking, if there are any (Khurana & Singh 2001; Salazar *et al.* 2011; 2012b). Understanding seed germination traits helps determine which species are most likely to persist after a disturbance and important for vegetation management and conservation of genetic resources (Primack 1990). In addition, it allows fast-growing species, along with species with potential seed bank formation that germinate over time, to contribute to in situ and ex situ restoration and conservation efforts (Merritt & Dixon 2011). Therefore, restoration strategies in these environments can stimulate the formation of heterogeneous seed banks, enabling secondary recruitment. The target species used in restoration need to be tested to determine whether they remain viable in seed banks. Hence, our aim was to evaluate germination under darkness simulation in direct seeding conditions, the effect of seed dormancy breakage on germination and its cost-effectiveness, as well as the seed bank formation of some key species that could potentially be used in Cerrado restoration.

Materials and methods

Species

Considering that the Cerrado biome contains different types of native vegetation, we selected species that occur in both savannas and forests (*i.e.*, generalists), as well as species that occur exclusively in savannas (*i.e.*, savanna specialists) or forests (*i.e.*, forest specialists) (Abreu *et al.* 2017) (Tab. 1). We attempted to select species that are commonly sold in seed markets. The seeds were purchased from the 'Instituto Brasileiro de Florestas' (IBF https://www.ibflorestas.org.br/) and the 'Rede de Sementes do Xingu' (https://www.sementesdoxingu.org.br/site/home/). All seeds purchased originated from the current annual harvest (<1 year of storage) and were processed manually/induced in the laboratory.

Germination

We conducted a germination test for 42 days in the laboratory, using 100 seeds from each species, distributed in four replications of 25 seeds each (Kildisheva *et al.* 2019). We germinated seeds in Petri dishes with filter paper moistened with 1 % nystatin solution (Garcia *et al.* 2006). The plates were kept at a constant temperature of 25 °C. Since a thin layer of soil is usually used to cover seeds in direct seeding, we conducted germination tests in the dark to simulate dark soil conditions in the field. We counted germination on the plates everyday under a green safelight using root protrusion as a germination criterion.

Table 1. List of native species, regional names, and habitat preference (Durigan *et al.* 2004;2012; Mendonça *et al.* 2008; Abreu *et al.* 2017) used for germination and seed bank experiments in APA Guariroba in Campo Grande, Mato Grosso do Sul, Brazil.

Family	Scientificname	Regional name	Habitat preference
Anacardiaceae	*Astronium fraxinifolium* Schott	gonçalo-alves	generalist
Apocynaceae	*Aspidosperma subincanum* Mart.	peroba-do-cerrado	savanna
Bignoniaceae	*Tabebuia roseoalba* (Ridl.) Sandwith	ipê-branco	forest
Urticaceae	*Cecropia pachystachya* Trécul	Embaúba	generalist
Combretaceae	*Terminalia corrugata* (Ducke) Gere & Boatwr.	boca-boa	generalist
Euphorbiaceae	*Mabea fistulifera* Mart.	mamoninha, leiteiro	generalist
Fabaceae	*Anadenanthera colubrina* var. *cebil* (Griseb.) Altschul	angico-cuiabano	generalist
	Copaifera langsdorffii Desf.	pau-d'óleo-de-copaíba	generalist
	Dimorphandra mollis Benth.	faveiro	savanna
	Dipteryx alata Vogel	baru, cumbaru	generalist
	Hymenaea stigonocarpa Mart. ex Hayne	jatobá-do-cerrado	savanna
	Peltophorum dubium (Spreng.) Taub.	canafístula	generalist

Dormancy breakage and its cost-effectiveness

Of the species used in this study, we identified four with tegument impermeability dormancy - *H. stigonocarpa* (Pereira *et al.* 2011), *P. dubium* (Oliveira *et al.* 2008), *C. langsdorffii* (Pereira *et al.* 2013), and *D. mollis* (Salomão *et al.* 2003). Dormancy breakage was achieved through thermal shock, using boiling water at 60 ºC for five minutes and then an ice bath for one minute. Hence, for these species with hard seed coat structure, suggesting seed integumentary dormancy traits, after a thermal shock, we carried out a germination test again to compare it, under the same conditions, with results of the germination test without dormancy breakage conditions.

Based on our results, we compared cost scenarios between overcoming seed dormancy (100 % of seed lot - yes) or not (0 % - no), considering seed availability in the market; seed price per kilo found in the market; seed amount kg/ha based on Reis *et al.* (2019); labor cost/ha to overcome seed dormancy; total cost/ha in both scenarios (with and without seed dormancy breaking); percentage of germination found in our study; and increasing or decreasing magnitude of germination after seed dormancy-breakage (*i.e.*, dividing the percentage of germination without seed dormancy-breakage by the percentage germination with seed dormancy-breakage) (see an overview of the calculations in Tab. S1 in supplementary material).

Seed bank formation

To evaluate the seed bank formation, we used 200 seeds per species, which were arranged in fine-mesh nylon bags (20 per species) and buried about 5 cm deep (Fig. 1A) (Velten & Garcia 2007) at the same site that Reis *et al.* (2019) used for direct seeding experiments by (Fig. 1B). The nylon bags were taken to the field and randomly buried in previously selected areas on the Velho Saltinho (20º34'45. 41" S, 54º21'44" O) farm in the Mananciais do Córrego Guariroba Environmental Protection Area in Campo Grande, Mato Grosso do Sul, Brazil. All these seeds were not previously treated for dormancy breaking. After being buried for six months, we unearthed the bags (Fig. 1C, D) and performed the germination test in the laboratory again, under the same conditions as the previous test, to compare buried and non-buried seeds.

Data analysis

We calculated the percentage of species germination. We compared the species with hard seed coat structure that suggested seed integumentary dormancy traits to germination data after thermal shock. Moreover, we compared the germination percentage before and after seeds were buried for six months using the formula: $G = \Sigma n_i / N \times 100$, where n_i is the number of seeds germinated and N is the number of seeds in each Petri dishes (Labouriau 1983). To determine the germination velocity of each species, we calculated average germination time (t–), which is an indication of germination process velocity; $t\text{-} = \Sigma (n_i \times t_i) / \Sigma$, where n_i is the number of germinated diaspores per day and t_i is the day they germinated (Labouriau 1983). The seeds were classified into three categories: rapid twinning (< five days), intermediate germination (five <t - <10 days), and slow germination (> 10 days) (Ferreira *et al.* 2001). After testing the data distribution and finding parametric distribution, the means were compared to the one-way analysis of variance (ANOVA) and Tukey post-hoc test ($p < 0.05$) in the R program (R Development Core Team 2018).

Results

Germination

The seeds that were not subjected to dormancy breakage and not buried for six months, 10 of the 12 species germinated in 40 days, ranging from 95 % for *A. colubrina* to 10 % for *H. stignocarpa* (Fig. 2). *A. fraxinifolium*, *C. langsdorffii*, and *D. alata* showed more than 50 % germination and *P. dubium* presented 46 % germination in the same period (Fig. 2). *T. roseoalba*, *D. mollis*, *M. fistulifera*, and *C. pachystachya* had lower germination rates, ranging from 10 to 29 % (Fig. 2). *A. subincanum* and *T. corrugata* did not germinate.

For *A. colubrina* and *A. fraxinifolium*, germination started on the first day and reached maximum germination rates after ten days (Fig. 2). *Peltophorum dubium* and *C. pachystachya* took about 15 days to reach their maximum germination rates (Fig. 2). *D. mollis* started to germinate between 0-5 days and reached peak germination between 15 and 20 days (Fig. 2). *Copaifera langsdorffii* and *D. alata* took about 20 days to stabilize their germination rates (Fig. 2), while the other species took longer to germinate.

Dormancy breakage and its cost-effectiveness

For seeds that were subjected to dormancy breakage, *D. mollis*, *H. stigonocarpa*, and *P. dubium* showed an increase in germination rates after dormancy break (Fig. 3). However, the germination rate of *C. langsdorffii* decreased from 56 % to 32 % after seed dormancy breakage treatment, which is 1.8 times lower (Fig. 3). The total amount of money that could be saved is<~US$4-5/ha for some species (*P. dubium* and *D. mollis*, respectively) and ~US$50/ha for *H. stigonocarpa* (Tab. S1, and see values in "Reais" in supplementary material).

Seed bank formation

After digging up the nylon bags that were buried for six months, we found seeds of *D. mollis* (one with live radicle and six with dead radicle), *M. fistulifera* (ten seeds with dead radicle), *T. corrugata*(ten seeds with dead radicle, one seed with live radicle, and seven live seedlings) and *H. stigonocarpa* (ten seeds with dead radicle and one live

seedling) (Fig. 1). Additionally, we verified that only *C. pachystachya*, *D. mollis*, *H. stigonocarpa*, and *M. fistulifera* had enough seeds for the germination test. The other eight species had predated/deteriorated seeds (Fig. 1D).

Cecropia pachystachya doubled its germination percentage from 10 % to 30 % and *H. stigonocarpa* presented the largest difference, with a germination rate rising from 10 % to 50 % after being buried. Although *M. fistulifera* and *D. mollis* did not germinate in the experiment (<2 %) (Fig. 4), we found germinated seeds after digging up the nylon bags (Fig. 1).

Average germination time (t-)

On average, the germination period ranged from 5 to 25 days (Fig. 5). The t- of species that were neither treated nor buried in the seed bank (n=10 species) varied from species to species (Fig. 5A). Among these, *T. rosealba* (23), *H. stigonocarpa* (23), *M. fistulifera* (12), *C. langsdorffii* (15), and *C. pachystachya* (15) presented the highest average germination times (Fig. 5A). *A. colubrina* presented the lowest t- (Fig. 5A). The seeds that were treated for dormancy breakage were only different when compared to untreated *H. stigonocarpa* seeds (Fig. 5B). *H. stigonocarpa* and *C. langsdorffii* had a longer germination period compared to the other species (Fig. 5B), and the germination period for *H. stigonocarpa* was lower when there was dormancy breaking (eight days of difference). The opposite happened for seeds of this species that were buried, with seeds in the seed bank (after being buried for six months) presenting a higher average t- (three to seven days longer) than untreated

Figure 1. Seed bank formation test. **(A)** a pit where nylon bags were buried, **(B)** nylon bag with seeds before being buried, **(C)** nylon bag unearthed after 6 months, and **(D)** nylon bag unearthed after 6 months with predated/deteriorated seeds.

seeds (without burying) (Fig. 5C), whereas burying *D. mollis* seeds increased its germination, while *M. fistulifera* did not germinate when buried (Fig. 5C).

Discussion

Germination and Average Germination Time

More than 50 % of *A. colubrina*, *A. fraxinifolium*, *C. langsdorffii*, and *D. alata* seeds germinated in less than 40 days (T50 ≤ 40 days). Among the studied species, *A. colubrina* and *A. fraxinifolium* were the fastest germinating species (T50 < 10 days). Serpa *et al.* (2010) and Oliveira *et al.* (2012) also observed the highest average germination rates and germination times for *A. colubrina*. Results suggest high reproductive vigor for these species due to accelerated and high germination in wide temperature ranges, with no seed dormancy (Maia 2004). This phenomenon differs from that observed for *H. stignocarpa, P. dubium, C. langsdorffii*, and *D. mollis,* which are species that presented low germination rates and longer times due to their integument dormancy (Salomão *et al.* 2003; Oliveira *et al.* 2008; Pereira *et al.* 2011; 2013). Improving germination performance may demand

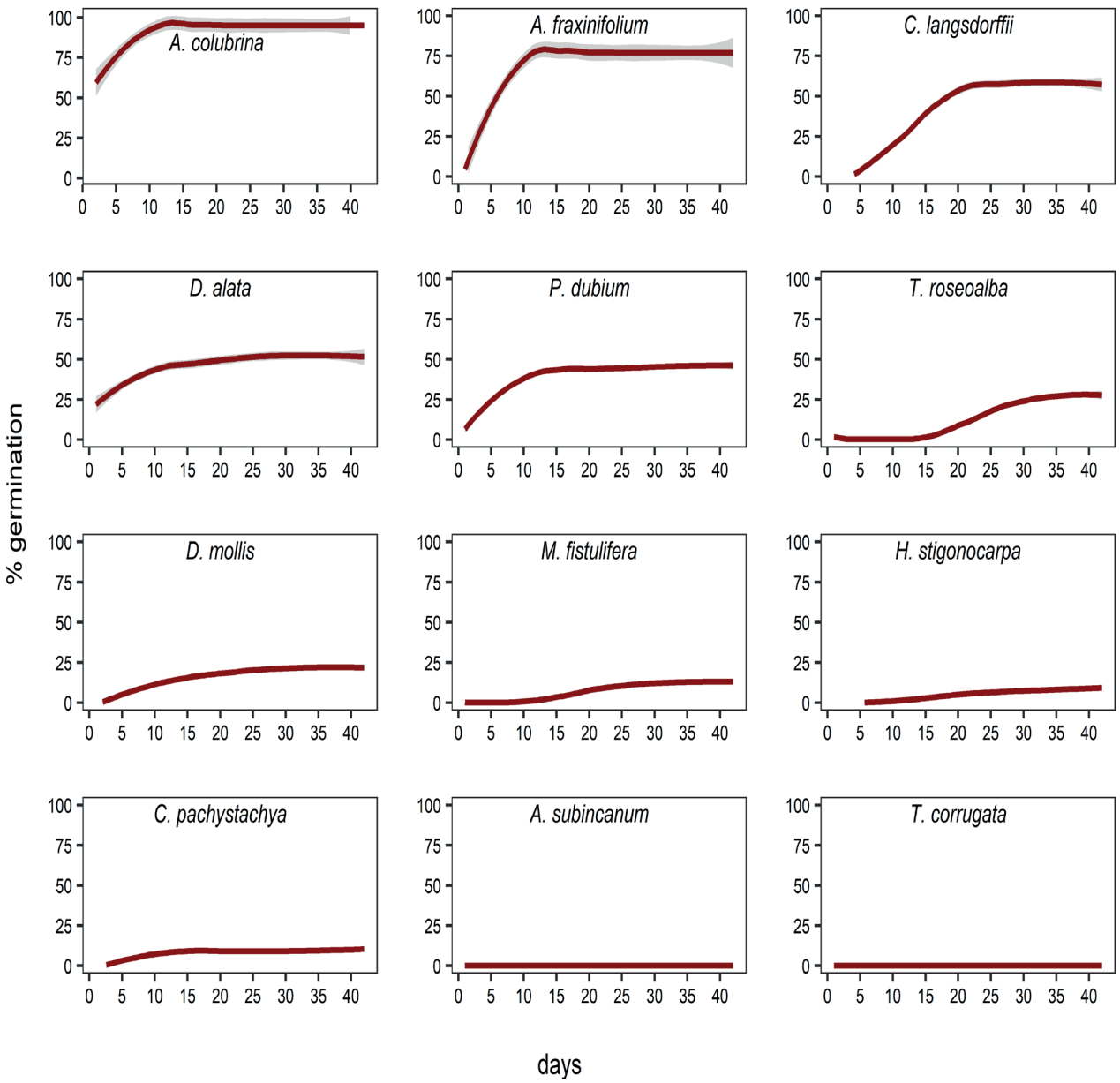

Figure 2. Percentage of germination in the laboratory (at 25 °C in the dark for 42 days) of native species commonly used to restore woody communities by direct seeding in the Cerrado biome.

a species-by-species approach to re-establish the native plant community in restoration sites (Elzenga *et al.* 2019).

Non-germination of *A. subincanum* and *T. corrugata* species in the laboratory may be related to the seed lot, type of photoblastism or low seed storage potential, which can reduce seed viability (*e.g.*, *A. subincanum*, Oliveira *et al.* 2016). Previous experiments suggest that *A. subincanum* has optimal germination at 25 °C and a 12-hour photoperiod (Oliveira *et al.* 2016), while 100 % of *T. corrugata* seeds can germinate in natural temperature and light conditions (Soares *et al.* 2006; Farias *et al.* 2015). Therefore, regarding treatment homogeneity, the germination test simulating darkness of buried seeds and direct sowing conditions shows that direct seeding strategies must also be heterogeneous in the field. Hence, considering photoblastism, with some species germinating only in darkness, others in light and others indifferent, heterogeneous strategies for direct seeding (*e.g.*, a thin layer of soil over seeds in some parts of the furrow and not in others) could be tested further.

Dormancy breakage

Germination of *C. langsdorffii* seeds decreased after thermal shock, therefore this technique cannot be recommended for germination of this species. Silva *et al.* (2016) also came to such conclusion after finding that chemical scarification after immersion in sulfuric acid for 10 minutes was the best treatment. Another interesting option is partial seed burial and subsequent burning for 30 minutes, as fire could be a key factor for enhancing germination, with better results found for this species (Souza *et al.* 2015).

Conversely, the dormancy suppression of *P. dubium*, *D. mollis*, and *H. stignocarpa* seeds by thermal shock was successful, reflecting high germination percentage. This thermal shock can occur under natural conditions in the Cerrado because of recurring disturbance events during the dry and cold winter (Soares *et al.* 2006). However, when correlating the germination percentage to the average

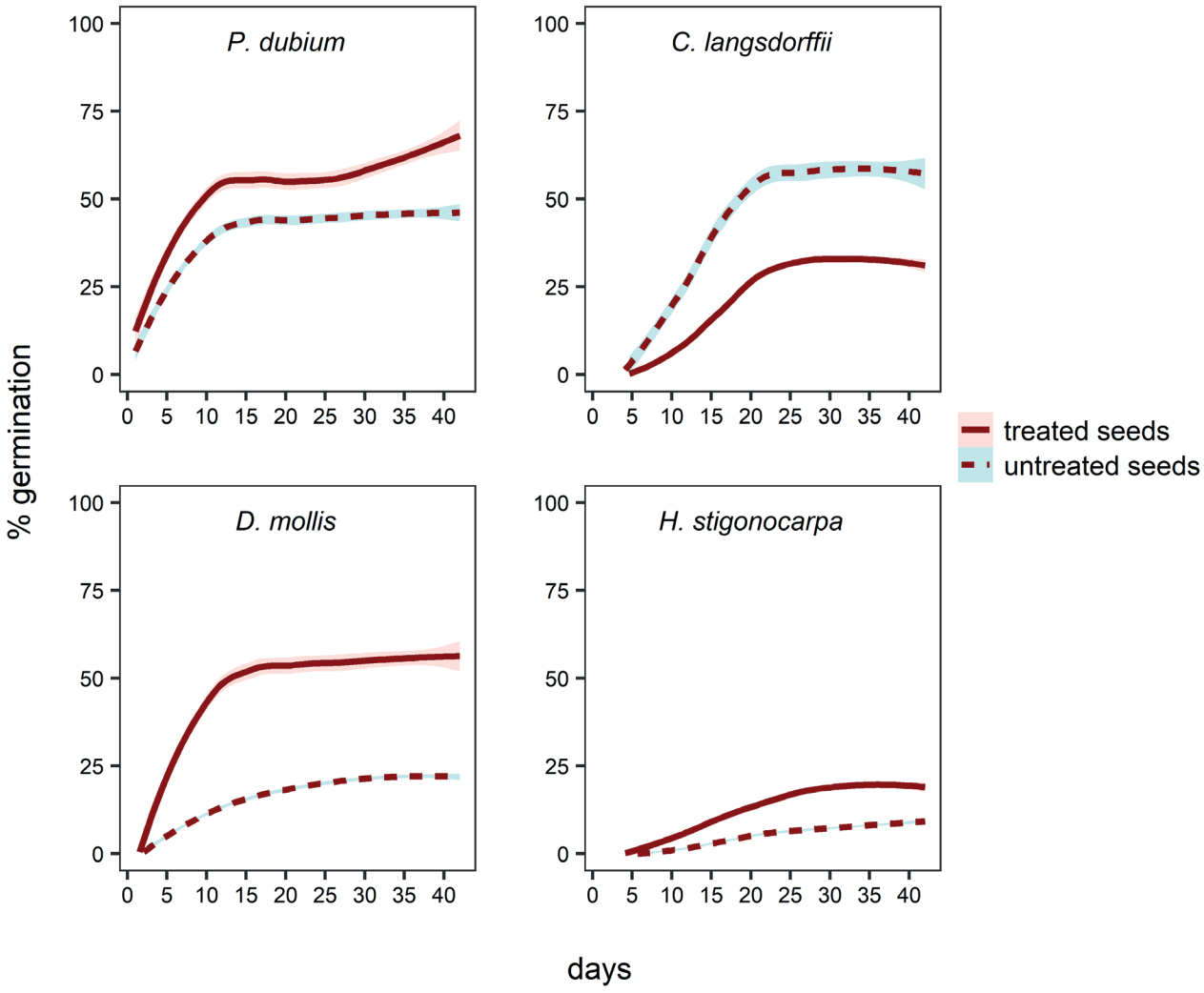

Figure 3. Comparison of germination percentage of native species with (treated seeds) and without dormancy overcoming treatment by thermal shock (untreated seeds).

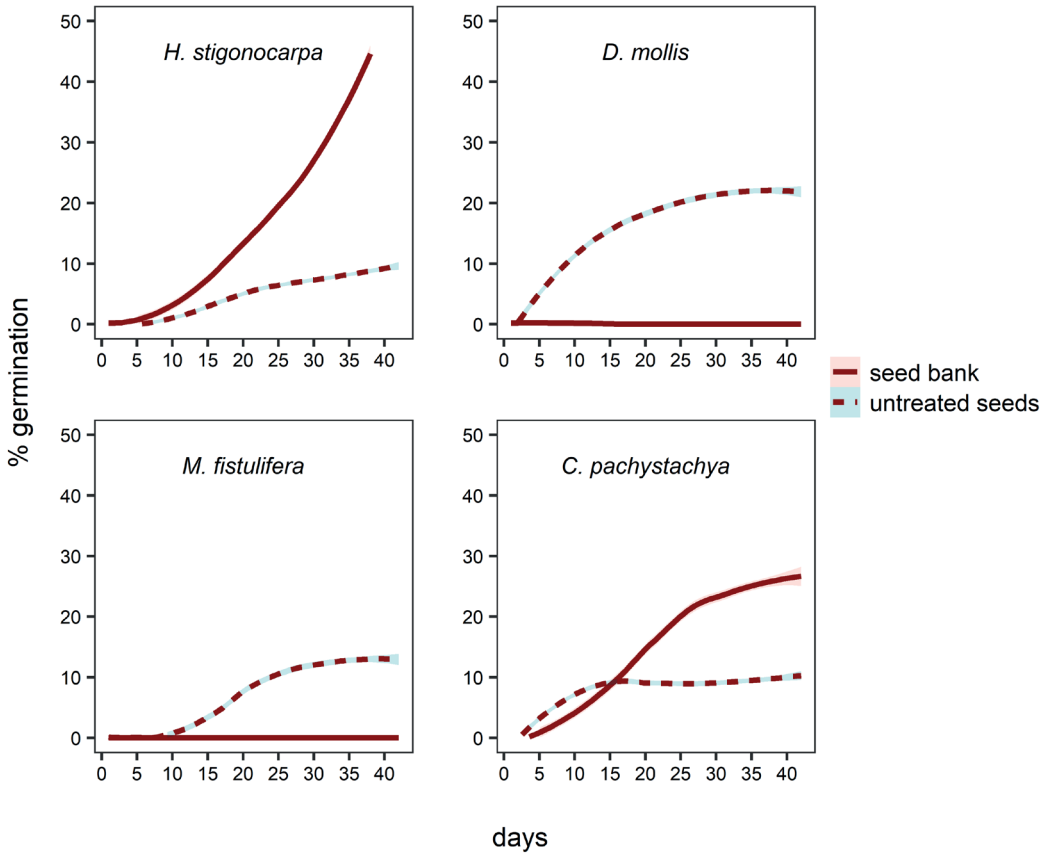

Figure 4. Comparison of native species germination percentage without dormancy overcoming treatment (untreated seeds) and after being buried for six months.

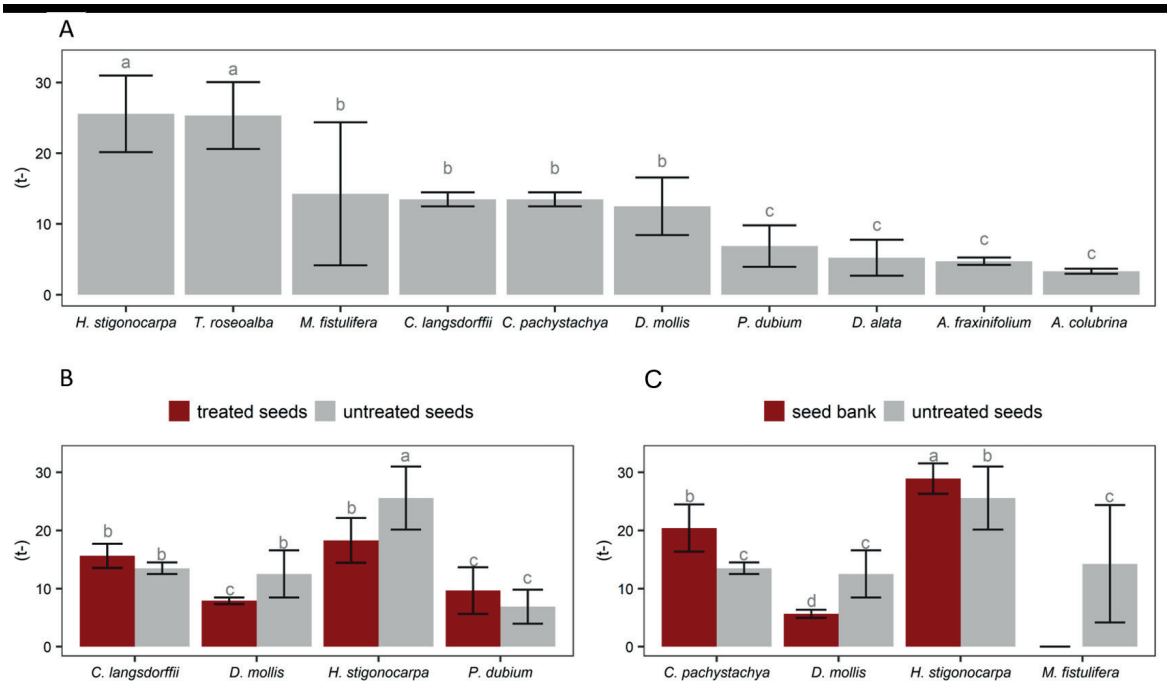

Figure 5. Average time of seed germination (t-) in days of all evaluated species. **(A)** germination test of species without test of seed dormancy breaking and seed bank; **(B)** of species that we tested dormancy breaking; **(C)** of species that we tested seed bank after being buried for six months. *Species whose germination value was 0 was not added to the charts (*Aspidosperma subincanum* and *Terminalia corrugata*). Values followed by the same letter do not differ between the Tukey test at 5 % of significance

germination period (days), seed treatment is not so feasible. The difference in germination period may not be significant in the long run, which can postpone the growth of the established individuals, as well as the canopy closure for forest vegetation types. In addition, the operational effort of dormancy-breaking may not be worthwhile for the species studied herein. Since those species have high potential for ecological restoration, an alternative that can compensate for dormancy-breaking is to increase the density of seeds at the time of sowing, but only if that strategy would reduce implantation costs. This decision should be based on the attributes of the species planted. In some cases, dormancy-breaking could be a disadvantage as it could increase the risk of seedling mortality from water stress during the dry season (Zaidan & Barbedo 2004) or an unexpectedly long drought in the wet season. Additionally, planting seeds without dormancy-breaking could increase seedling survival under microclimate oscillations (Mcivor & Howden 2000; Azania *et al.* 2003; Tunes *et al.* 2009).

Considering the contrasting results, which depend on the species response, and for logistical purposes, we recommend overcoming dormancy to increase the seed germination rate or seed density depending on key decision criterion. Our study showed that dormancy-breaking enhanced germination in three of the four species tested, however, depending on labor costs of seed dormancy-breaking and seed availability, it may or may not be worthwhile to break seed dormancy (see Tab. S1 in supplementary material). Future studies could test part of the seed lot and take seed costs into consideration to evaluate this key decision criteria approach. The seed dormancy-breaking test is simple and inexpensive since it only uses a few parts of the seed lot (*e.g.*, 200 seed = 100 for dormancy-breaking test and 100 as a control). Hence, based on seed cost, seed availability (species rarity or seed market availability), and labor availability (skilled labor or time to commit to dormancy-breaking), the practitioner could decide the best option for each species (*e.g.* Table S1 in supplementary material). Although the total amount of money saved is very low (< ~US$4-5/ha) for some species, it is quite high and could be an interesting option for other species (*e.g.*, ~US$50/ha for *H. stigonocarpa*, Tab. S1 in supplementary material). Hence, when comparing the four studied species, the thermal shock technique is recommended for large-scale direct seeding if the only intention is to enhance germination of *H. stignocarpa*. Even though we only tested germination in the laboratory, our results indicate that standardizing direct seeding in the field may not benefit all species equally because of the differences between species attributes and the distinct conditions required for successful emergence and establishment (Montalvo *et al.* 2002; Kiehl *et al.* 2010).

Seed bank formation

Only two species were able to form a seed bank, which germinated after six months underground (*C. pachystachya* and *H. stigonocarpa*). Additionally, we also found live seedlings of *T. corrugata* and *H. stigonocarpa* inside buried nylon bags acting as transient seed bank builders, according to Thompson *et al.* (1993). This classification encompasses species whose seeds remain in the soil for up to one year. However, it is possible that *C. pachystachya* and *H. stigonocarpa* seeds remain in the soil longer, thus long-term investigations are necessary. *Cecropia* seeds are commonly found in abundance in seed banks, as their small size facilitates seed displacement in the litter, which is eventually incorporated into the soil (Chambers *et al.* 1991; Guo *et al.* 2000; Souza 2003).

Our most interesting result is that *H. stigonocarpa* germination rates increased sharply (almost fourfold) after six months underground. The seed bank is extremely important in nature and in restoration processes for environmental resilience (Tres *et al.* 2007). The increased germination potential from 10 % to 45 % after soil incorporation for six months could be a strategy to initially reduce intraspecific competition for resources since there is a high rate of seed germination after direct sowing. The possibility of continuous germination over time, could enhance species survival even after stochastic events (Tres *et al.* 2007) such as droughts.

Our results show that *A. colubrina, A. fraxinifolium, C. langsdorffii*, and *D. alata* had the highest germination rates and are indicated for restoration projects that seek to quickly establish species. *P. dubium* and *D. molis* also had high germination rates after dormancy break and are also indicated for restoration projects. Only *H. stigonocarpa* and *C. pachystachya* showed seed bank formation potential, as well as signs that they remain active for over a year. When used in direct seeding with other species, these two species support the temporal dynamics of restoration. Considering the differences in germination responses of native species, we recommend applying dormancy-breaking in a portion of the seed lots when there is not enough information about a species, as it could provide heterogeneous results for direct seeding. In addition, we highlight that the species with low germination rates presented in this study should not be excluded from restoration activities and need to be further investigated. These species could be used to increase diversity, but to enhance their establishment the number of seeds need to be increased at the beginning of the project based on the goals of the restoration project, and available resources.

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