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Less is more: Little seed processing required for direct seeding in seasonal tropics

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Abstract
Seed processing and dormancy break treatments are recommended for rendering seeds restoration-ready. Conversely, fruit structures and seed coats may protect seeds from environmental harm in the field. We evaluated the effects of seed processing (by either keeping fruit structures or extracting seeds) and/or scarification (of physically dormant seeds) on the seedling emergence and establishment of 10 legume tree species from tropical forests and savannas of Central Brazil. We sowed seeds in a greenhouse for reference and in a field experiment conducted in tilled ready-to-seed sites. We monitored seedling emergence and survival for a year. We calculated the costs of harvesting, processing, and pretreating seeds, and considered the final cost of a 1-year-old seedling. Seed extraction resulted in lower emergence for most species in the greenhouse and in the field. It also accelerated emergence of three and four species in the greenhouse and the field, respectively. Scarification resulted in lower seedling emergence in the field for half of the species, while it increased emergence of three species in the greenhouse. Most species presented accelerated emergence both in the greenhouse and the field. The seedling cost was 1.6 to 74.6 times higher when seeds were processed, and 1.3 to 6.0 times when seeds were scarified, except for one species. Keeping fruit structures and seed coats reduced the costs of seeds and increased the success of direct seeding.

Keywords Cerrado · Seasonal tropical forest · Ecological restoration · Fabaceae · Seed dormancy · Seed processing

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Introduction

Direct seeding for ecological restoration has been highly improved and increasingly used recently for seasonally dry ecosystems (Pérez et al. 2019; Sampaio et al. 2019; Raupp et al. 2020). Direct seeding is cost-effective for restoration compared to nursery-grown tubestock planting, since the low direct seeding costs compensate for its low seedling establishment rates (Masarei et al. 2019; Pérez et al. 2019; Raupp et al. 2020). Another advantage of direct seeding is that it promotes a fast vegetation recover due to the high sapling densities resulted from high seeding density (Meli et al. 2018; Freitas et al. 2019), and because direct seeding incorporates fast-growing herbs and shrubs (Freitas et al. 2019; Sampaio et al. 2019).

A series of technical improvements are still needed to enhance the cost-effectiveness, as well as the species (and functional) diversity that is achieved with direct seeding. Seeds comprise the highest cost of direct seeding, with seed processing (i.e. grading, cleaning, extracting from fruits, and depulping) being the main cost component for many species (Raupp et al. 2020). Seed processing increases the germination potential of the seed lot as it removes damaged propagules, impurities, and lining structures, such as wings and shells which can attract pathogens and predators (Mijnsbrugge et al. 2010). It also improves seed handling through the seed supply chain, and facilitates the passing of seeds through mechanical seeders (Frischie et al. 2020). Therefore, a carefully managed seed-supply chain that incorporates rigorous seed processing is desired (Frischie et al. 2020), if it is cost-effective.

It is often assumed that laboratory and greenhouse protocols of seed processing and dormancy break for germination and seedling production are applicable to direct seeding restoration (Kildisheva et al. 2020; Passaretti et al. 2020). Dormancy break promotes synchronization and acceleration of germination, which are desirable characteristics for seedling production (Pedrol et al. 2018). However, such manipulation could negatively affect germination in the field for certain species. In fact, structures such as shells, wards, and chambers, as well as seed tegument could protect seeds from predators, and mitigate seed exposure to extreme to soil surface desiccation and high temperatures found in the ready-to-seed sites. Desiccation is a major mortality cause at the germination and seedling stages in seasonally dry forests and savannas, where dry spells are frequent along the rainy season (Woods and Elliott 2004; Vieira et al. 2008; Ribeiro and Borghetti 2014). It is also one of the biggest bottlenecks of direct seeding in seasonal ecosystems (Silva et al. 2015; Silva and Vieira 2017). In fact, slow-paced germination is a strategy to await better soil moisture conditions, and as a bet-hedging strategy (Garwood 1983; Simons and Johnston 2006; Vieira et al. 2008; Ribeiro and Borghetti 2014). On the other hand, dormancy break treatments allow seedlings to grow earlier and get a head start in the competition with weeds after germination, while using dormant seeds would lead to an extended weed control on restoration sites (Woods and Elliott 2004; Grossnickle and Ivetić 2017). Therefore, it is necessary to know the species biology as well as the environment to be restored before deciding on pretreating seeds.

Fabaceae (Leguminosae) is a dominant family in successional and mature seasonal tropical forests (Gei et al. 2018) and savannas (Pellegrini et al. 2016), and is prevalent in direct seeding forest restoration. Legume seeds are mostly orthodox (desiccation-tolerant) and physically dormant (impermeable seed coat), thus suitable for storage until the sowing season (Rodrigues et al. 2019). In this study, we evaluated the effect of seed extraction from fruits and/or seed scarification treatments, usually recommended for germination in laboratory conditions, on the emergence and establishment of seedlings of 10 legume tree species in the field. We sowed seeds in the field, as well as in a greenhouse to have a reference for emergence responses under optimal conditions. We hypothesized that seed processing and scarification could decrease seedling emergence in the field, compared to unprocessed seeds, whose fruit structures and seed coats would protect embryos from extreme temperatures and moisture fluctuations in the tropical seasonal restoration sites. In addition, we expected that seed processing and scarification would accelerate and synchronize seedling emergence, resulting in increased mortality during the rainy season due to desiccation or predation in the restoration sites. However, seedlings that emerged earlier and managed to survive would be bigger at the end of the rainy season than seedlings that emerged later, leading to a higher survival of the older seedlings during the following dry season. Finally, because establishment success increases with seed size, as both seeds and seedlings from large seed species are more resistant to desiccation (Camargo et al. 2002; Tunjai and Elliott 2012; Silva and Vieira 2017; Passaretti et al. 2020), among other ecological filters, we expected that the negative effects of seed extraction and scarification in the direct seeding would decrease with increasing seed size.

Materials and methods

Study area, species and treatments

The study was carried out from December 2016 to December 2018 in the Southeast of Goiás state, in Central Brazil. The region is located in the Cerrado biome, where savannas and scleromorphic forests occur on arenitic soils, semideciduous forests on basaltic soils, and deciduous forests on granitic or gneissic shallow soils (BRASIL 1983). The landscape includes flat ridge tops and V-shaped valleys. The altitude is 650–750 m. The average annual rainfall is 1510 mm, with 93 % of the rainfall occurring between October and April. The average temperature ranges from 19 °C in July to 25 °C in December (compiled from hidroweb.ana.gov.br). The onset of the rainy season is generally in October/November, but constant rains and adequate soil moisture are reached in December.

We studied ten Fabaceae trees typical of savannas and seasonal forests of Central Brazil (Ratter et al. 2003; Table 1; species will be referred to by their genus). The species are slow-growth, heliophyte trees, except for *Tachigali rubiginosa*, which is a fast-growth tree. The species occur from open to closed savannas (cerrado stricto sensu), scleromorphic forests (cerradão), and transitional mosaics with seasonal forests (consulted at the Brazilian species traits database WebAmbiente—https://www.webambiente.gov.br/). Fruits were collected in 2016 and 2017 from 15 parent trees per species, with a trimmer or directly from the ground, in the municipalities of Catalão, Campo Alegre, and Davinópolis, along the São Marcos River basin (Goiás state, Brazil). Seeds were stored at 15 % humidity, 18 °C for 3–5 months. The direct sowing experiment in the field was carried out in two sites distant 12 km from each other. Site 1 (18° 0’12’’S / 47°38’40’’O; 763 m a.s.l.) was seeded in December 2016, with *Tachigali*, *Dipteryx*, and *Vatairea*. Site 2 (17°59′54″ S / 47°45’46’’ O; 764 m a.s.l.) was seeded in December 2017, with *Dimorphandra*, *Hymenaea*, *Stryphnodendron*, *Bowdichia*, *Plathymenia*, *Platypodium*, and *Machaerium*.

Collected fruits and seeds were selected based on their quality, and were extracted from fruits and scarified for dormancy breaking, depending on the species biology (Table 1; Fig. 1). For six species, we tested both keeping fruit structures and extracting

Table 1 Species studied, fruit and seed extraction description, treatments for seed extraction and seed scarification. For seed extraction, six species were tested, and for seed scarification, six species were also tested. Two species were tested both for seed extraction and seed scarification. Seed scarification was tested only for species with known physical dormancy, according to literature (literature is referenced for each species in the Table). Propagule mass (fruit and seeds) were calculated by weighting 1000 seeds. See Fig. 1 for photos of the fruits and seeds. Species habitat are Savanna (S) and Forest (F)

Species	Habitat	Fruit description[a]	Seeds per fruit	Propagule mass (g)	Seed extraction technique	Treatments of seed extraction	Treatments of seed scarification
Dipteryx alata Vogel	S,F	Indehiscent drupoid fruit, fleshy epicarp[b]; woody fibrous mesocarp and endocarp, poorly permeable with well-closed and cohesive fiber tissues.	1	Fruit: 22.48 Seed: 1.01	Seeds are extracted from the woody mesocarp and endocarp with a machete or an appropriate device.	Fruit Seed	No scarification
Machaerium opacum Vogel	S	Indehiscent samaroid fruit with a single wing and a chamber that surrounds the seed, poorly permeable chamber with partially cohesive fiber tissues.	1	Fruit: 0.61 Seed: 0.12	Seeds are extracted from wings with scissors or another device.	Winged fruits Seed	No scarification
Platypodium elegans Vogel	S,F	Indehiscent samaroid fruit with a single wing and a chamber involving the seed; poorly permeable chamber with cohesive fiber tissues.	1	Fruit: 1.13 Seed: 0.17	Seeds are extracted from wings with scissors or another device.	Winged fruits Seed	No scarification

Table 1 (continued)

Species	Habitat	Fruit description[a]	Seeds per fruit	Propagule mass (g)	Seed extraction technique	Treatments of seed extraction	Treatments of seed scarification
Vatairea macrocarpa (Benth.) Ducke	S,F	Indehiscent samaroid fruit with a single wing and a chamber involving the seed; poorly permeable chamber with partially cohesive fiber tissues and hydrophobic wax.	1	Fruit: 2.04 Seed: 1.03	Seeds are extracted from wings with scissors or another device.	Winged fruits Seed	No scarification
Plathymenia reticulata Benth.	S,F	Dehiscent coriaceous-epicarp; indehiscent, wing-like membranous endorcarp, segmented into monospermic sections, poorly permeable with cohesive fiber tissues.	11 ± 1[a]	Fruit: 0.06 Seed: 0.05	Winged (endocarp) seeds are easily detached from dehiscent fruits. Seeds are extracted from wings with scissors or another device.	Winged fruits Seed	Mechanical scarification[f] No scarification
Tachigali rubiginosa (Mart. ex Tul.) Oliveira-Filho	S,F	Crypto-samara; dehiscent coriaceous-epicarp; indehiscent endocarp, poorly permeable with well-cohesive fiber tissues.	1	Fruit: 0.13 Seed: 0.08	Seeds are beaten in a bucket with a nylon lawnmower, then separated manually.	Winged fruits Seed	Mechanical scarification[g] No scarification

Table 1 (continued)

Species	Habitat	Fruit description[a]	Seeds per fruit	Propagule mass (g)	Seed extraction technique	Treatments of seed extraction	Treatments of seed scarification
Bowdichia virgilioides Kunth	S,F	Samaroid-legume; indehiscent; thin and permeable pericarp with very loose fiber webs; rotting in contact with soil and water. Seeds have a small aril[c].	3 ± 1	Seed: 0.02	Fruits are macerated in a sieve until seeds come loose, residuals are blown away, and the remnants are put in water to select seeds; non-viable seeds float.	Seed extracted from winged fruit	Chemical scarification[c] No scarification
Dimorphandra mollis Benth.	S	Nucoid-legume; indehiscent; dry pericarp and fibrous mesocarp with a sweet caramel-like scent, attractive to frugivores[d].	14 ± 6	Seed: 0.19	Fruits are broken in a pestle, and seeds are separated manually or by passing through consecutive sieves.	Seeds extracted from the fruit	Mechanical scarification[h] No scarification
Hymenaea stigonocarpa Mart. ex Hayne	S,F	Nucoid-legume; indehiscent; dry pericarp and flour pulp mesocarp; attractive to frugivores[b].	5 ± 2	Seed: 4.18	Fruits are broken with a sledgehammer, the flour is separated in a pestle and sieve, then seeds are washed through a sieve.	Seeds extracted from the fruit	Mechanical scarification[h] No scarification
Stryphnodendron adstringens (Mart.) Coville	S	Nucoid-legume; indehiscent; dry pericarp and fibrous mesocarp with scent; attractive to frugivores[e].	8 ± 2	Seed: 0.08	Fruits are broken in a pestle, and seeds are separated manually or by passing through consecutive sieves.	Seeds extracted from the fruit	Mechanical scarification[i] No scarification

a. Information extracted from (Barroso et al. 2004), except for the specific information referenced with letters. b (Kuhlmann 2018a). c (8 min in sulfuric acid 98 %, de Albuquerque et al. 2015). d (Bizerril et al. 2005). e (Kuhlmann 2018b). f (Lopes et al. 2010). g (Carvalho and Figueirêdo 1991). h (Pereira et al. 2013). i (Martins and Nakagawa 2008)

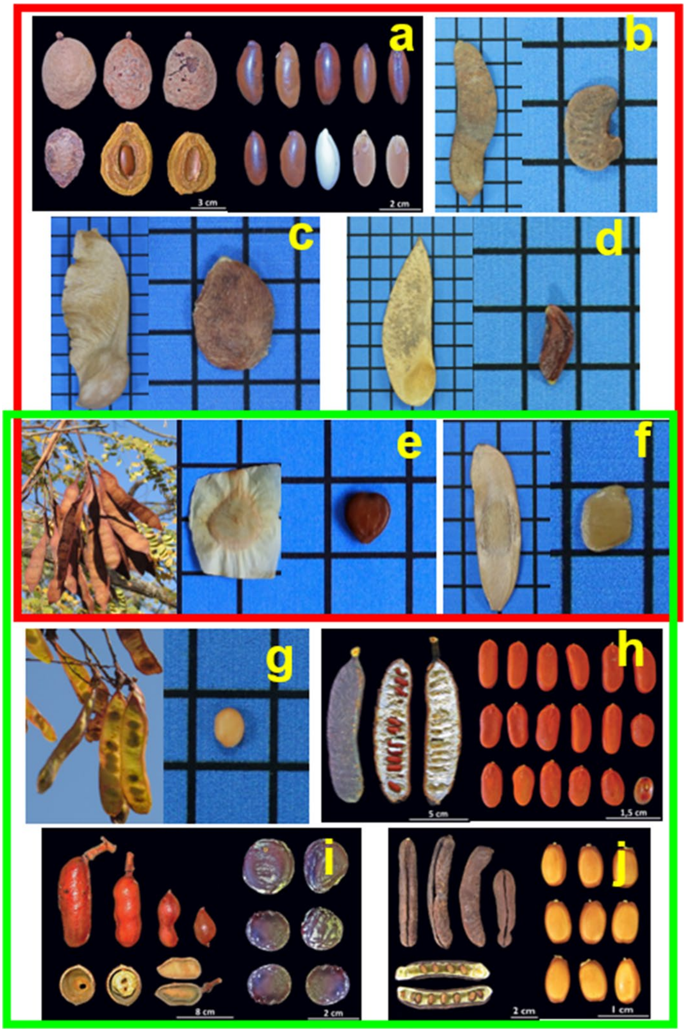

Fig. 1 Fruits and seeds of **a** *Dipteryx alata*, **b** *Machaerium opacum*, **c** *Vatairea macrocarpa*, **d** *Platypodium elegans*, **e** *Plathymenia reticulata*, **f** *Tachigali rubiginosa*, **g** *Bowdichia virgilioides*, **h** *Dimorphandra mollis*, **i** *Hymenaea stigonocarpa*, **j** *Stryphnodendron adstringens*. Red contour encompasses the species tested for sowing non-extracted × extracted seed. Green contour encompass species tested for intact seed × scarified seed. Photos a, h, i, and j were kindly provided by Marcelo Kuhlmann

seeds (extracted seeds vs. non-extracted seeds), considering species that display a single seed per fruit and also for *Plathymenia*, which has ~11 seeds/pod but each seed is individually enveloped by a papery endocarp (Table 1; Fig. 1; Warwick & Lewis 2003). Three of those species are commonly extracted from fruits for seed commercialization (*Dipteryx, Plathymenia*, and *Tachigali*), while the other three have samaroid (i.e. flattened wing, indehiscent) fruit (*Machaerium*, *Platypodium*, *Vatairea*) with a chamber that closely surrounds the seed (Barroso et al. 2004). The literature or standards for germination recommend either extracting seeds from fruits (for *Machaerium*, Rocha et al. 2003; for *Platypodium*, BRASIL 2013; for *Vatairea*, Fava 2014) or using the fruit itself as the germination unit (*Machaerium*, BRASIL 2013; *Platypodium*, Pacheco et al. 2007).

We tested scarification (yes vs. no) for species that present higher germination capacity in the laboratory when scarified, according to the literature (Table 1). That included two of the six species tested for seed extraction (*Plathymenia* and *Tachigali*) and other four study species (*Bowdichia*, *Dimorphandra*, *Hymenaea*, *Stryphnodendron*). As reference for optimal conditions, we recorded seedling emergence under greenhouse conditions and used the data as a control for field experiments.

Field and greenhouse experiments

Site 1 was an active African grass pasture (*Urochloa decumbens*) established on a mesotrophic woodland. In the year of the experiment, precipitation was 1,585 mm (data compiled from INMET - www.inmet.gov.br meteorological station of Catalão/GO). Site 2 was an old *Urochloa decumbens* pasture established in a dense savanna. Precipitation was 1,408 mm (data compiled from INMET - www.inmet.gov.br meteorological station of Catalão/GO). The soil is Red Argisol in Site 1 and dystrophic Oxisol (Red Latosol) in Site 2. Both sites were active pastures for decades, and cattle was removed for the start of the restoration experiments.

In both sites, the soil was prepared for seeding. The soil was tilled twice with a disc harrow for completely removing exotic grasses (in September-October), and for loosening and smoothing the soil to facilitate germination and seedling establishment (one day before seeding in December). The treatments were established in 1 m^2 plots. An iron frame with 100 cells of 10×10 cm squares was used as a template to seed 100 propagules of a given species. Thus, the exact position of a seed was known, allowing us to follow the fate of each propagule. Each seed management treatment (see Table 1) had four replicates of 100 propagules for each species. Seeds were buried at 1 cm depth.

The greenhouse experiments were conducted at the Federal University of Catalão, 34 km from the most distant field site. For *Vatairea* and *Dipteryx*, 25×30 cm plastic bags were used, and for the other eight species, seedling tubes (6.5×16 cm) were used. The substrate was composed of a 3:1:1 mixture of soil, bovine manure, and vermiculite. For each species and treatment, 25 propagules were sown, with four replicates. The greenhouse had automatic irrigation three times a day for five minutes at a time (8 mm/day in total), providing adequate moisture throughout the experiment. The replicates (25 propagules) were randomly distributed in the greenhouse. Each bag or tube was tagged for following the trajectory of each propagule. Once a month, weeds were removed from the plots in the field and from the greenhouse bags.

Monitoring

Seedling emergence and survival was observed every two weeks in the first two months and monthly up to six months in the field and the greenhouse. Then, seedling survival was noted after 12 months in the field. We considered seedling emergence when seedlings had exposed their cotyledons (for epigeal germination) or epicotyl (for hypogeal germination). Once a seedling was spotted, in the next censuses we verified whether it was alive or dead.

Seed and seedling costs

The cost of seeds and fruits used in the experiment was calculated by recording the costs of collecting and processing the propagules. We included the number of workers, time spent, and fuel used for collecting a known weight of propagules (for details see Raupp et al. 2020). We calculated the seed extraction and scarification treatments cost on a person-hour/seed weight basis. When there was chemical scarification, the cost of sulfuric acid was considered. Processing time was recorded for eight replicates of 100 propagules. Labor (person-hour) was converted into US$ 2.54/person-hour. Then we estimated the cost (US$) per seed. The cost of an established seedling 12 months after sowing was calculated by the cost of a propagule (fruit, seed, or scarified seed, depending on the treatment) divided by the proportion of seedling establishment (0 to 1) after 12 months of a propagule (also considering the treatment). The proportion of seedling establishment was calculated by the number of surviving seedlings (12 months after sowing) divided by the number of sowed seeds. Here we consider the effect of seed extraction treatments in the establishment success weighted by the propagule cost to estimate the cost-benefit relationship of processing seeds.

Data analyses

We ran separate analyses for seed extraction and seed scarification. For the response variables 'percentage', 'mean time', and 'synchrony of seedling emergence', factorial tests were run for the effects of 'species' (six species for both seed extraction and seed scarification treatments), 'seed extraction' (yes or no) or 'scarification treatments' (yes or no), and 'environment' (greenhouse or field). For the response variables, 'seedling survival' and 'seedling establishment' (number of surviving seedlings/sowed seeds), effects tested were 'species' (six species in each tray), 'seed extraction' (yes or no) or 'scarification treatments' (yes or no), and 'age' (6 and 12 months). We ran Generalized Linear Models (GLM) for each response variable, with a binomial distribution (logit function) for the count variables 'seedling emergence', 'seedling survival', and 'seedling establishment'; with a gamma distribution for 'mean time of emergence'; and with a gaussian distribution for 'synchrony of seedling emergence'. If an interaction between 'species', 'environment', and 'seed extraction' or 'scarification treatments' was significant, we compared the effect of seed extraction or scarification treatments for each species in each environment, since we were interested in the effects of the treatments in the field, having the greenhouse as a reference. Tukey tests were run for pairwise comparison.

To test the hypothesis that the negative effects of seed extraction and dormancy breaking in the field would decrease with increasing seed size, we run a linear regression model of the difference in percentage of seedling establishment in the field (extracted - non-extracted seeds; scarified - intact seeds) as a function of seed mass (log 10 transformed). All analyses were conducted using the R statistics program.

Results

Seedling emergence

Extracting seeds from fruits or removing seed wings resulted in lower emergence for four out of six species in the greenhouse and in the field, and in increased emergence for one species in the greenhouse and two species in the field (Fig. 2; see Table 4, "Appendix")

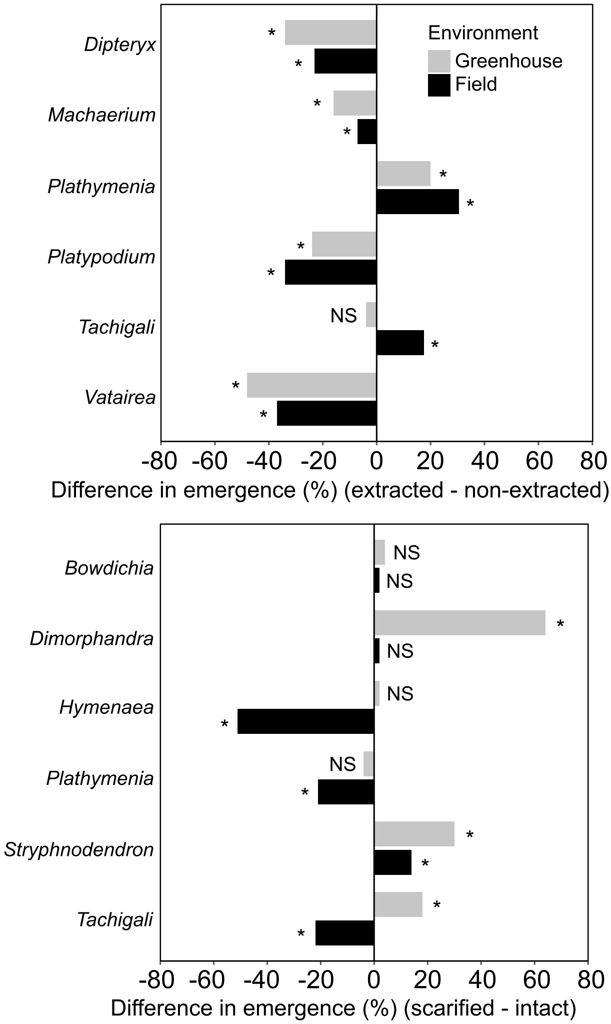

Fig. 2 Difference in the percentage of seedling emergence between **a** extracted and non-extracted seeds, and **b** scarified and intact seeds. Four tree species were submitted to each treatment, and two species were submitted to both treatments. Seeds were sowed in a greenhouse (frequent irrigation) and in ready-to-seed field environments. (*) Significant and (NS) non-significant differences between processed and unprocessed fruits, and treated and untreated seeds were verified with Tukey tests following the GLM results (see Table 4, Appendix)

for complete statistical analyses; see Table 5, "Appendix" for absolute data). Scarification resulted in lower seedling emergence in the field for three species, and in higher emergence for one species out of six species. On the other hand, scarification increased seedling emergence for three species in the greenhouse and had no influence on emergence of the other three species studied (Fig. 2; Tables 4 and 5, "Appendix").

Emergence time and synchrony

Under greenhouse conditions, seed extraction from fruits accelerated seedling emergence for three species, had no effect for one species, and hindered emergence for two species. Under field conditions, seeds extracted from fruits emerged more rapidly in the case of four species, and presented no effect in the case of two species (Fig. 3; Table 4, "Appendix" for complete statistical analyses). When seeds were scarified, five species presented accelerated emergence in the greenhouse and the field, and one species was indifferent to the treatment. The median time of seedling emergence was under 15 days for most seeds that were scarified and extracted from fruits, but our censuses intervals were 15 days (Fig. 3; Table 4, "Appendix). Besides accelerating seedling emergence, seed extraction and

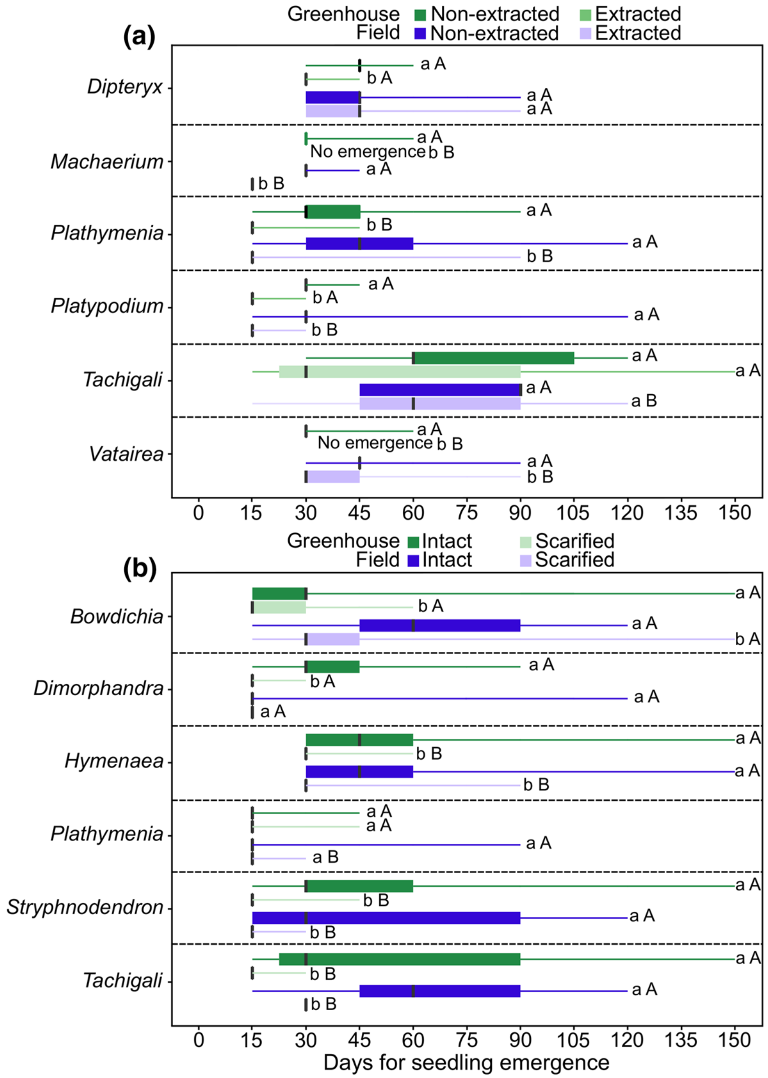

Fig. 3 Days for seedling emergence of **a** extracted and non-extracted seeds, and **b** scarified and intact seeds. Four tree species were submitted to each treatment, and two species were submitted to both treatments. Seeds were sown in a greenhouse (frequent irrigation) and ready-to-seed field environments. Values marked are the median, the quartiles, maximum, and minimum. The same letters above bars mean no significant difference between extracted and non-extracted seeds, and scarified and intact seeds for each species and environment (greenhouse and field). Lower case letters refer to the speed of germination, and capital letters refer to synchrony in germination time. Tukey tests were run following the GLM results (see Table 4, Appendix)

scarification treatments similarly "increased emergence synchrony, and accelerated seedling emergence (Fig. 3; Table 4, Appendix").

Seedling survival in the field

The percentage of surviving seedlings (surviving seedlings/emerged seedlings) at the end of the rainy season (ca. 6 months old) was lower when seeds were extracted from fruits for two species, higher for one species, and not different for three species. The same happened at the dry season (surviving seedlings at 12 mo/surviving seedlings at 6 mo; Fig. 4; see Table 4, "Appendix" for complete statistical analyses). Scarified seeds presented lower survival rates in the case of four species, and no change in survival in case of the other two species during the rainy season. In the dry season, scarified seeds had lower survival for two species, and no change for the other four species (Fig. 4; Table 4, "Appendix"). Seedling establishment (seedlings surviving 12 months after sowing divided by sowed propagules) is a combination of emergence and survival, and was used to calculate seedling costs (see Table 5, "Appendix" for absolute data). The effects of seed extraction and scarification treatments on seedling emergence and survival attributes are summarized in Table 2.

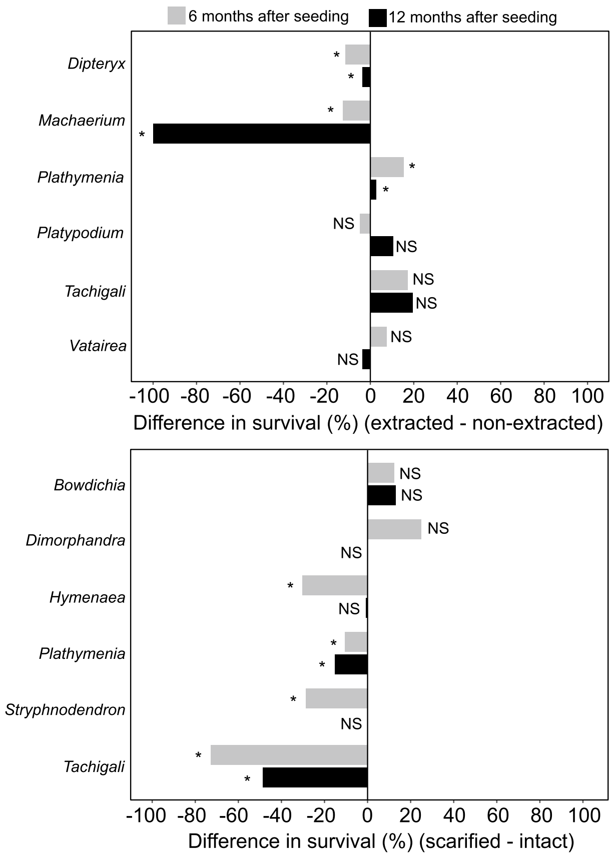

Fig. 4 Difference in the percentage of seedling survival between (a) extracted and non-extracted seeds, and (b) scarified and intact seeds. Four tree species were submitted to each treatment, and two species were submitted to both treatments. Seeds were sowed in ready-to-seed field environments, and survival was analyzed for seedlings 6 months after sowing (number of surviving seedlings at 6 months/number of emerged seedlings), and 12 months after sowing (number of surviving seedlings at 12 months/number of surviving seedlings at 6 months). (*) Significant and (NS) non-significant differences between extracted and non-extracted seeds, and scarified and intact seeds were verified with Tukey tests following the GLM results (see Table 4, "Appendix")

Table 2 Summary of the effects of seed extraction and seed scarification treatments for 10 species subject to direct seeding in the field

Species	Emergence			Field Seedling Survival		Establishment
	Percentage	Speed	Synchrony	6-mo	12-mo	12-mo old
Seed extraction						
Dipteryx alata	–	N.S.	N.S.	–	–	–
Machaerium opacum	–	+	+	–	–	–
Plathymenia reticulata	+	+	+	+	+	+
Platypodium elegans	–	+	+	N.S.	N.S.	–
Tachigali rubiginosa	+	N.S.	–	N.S.	N.S.	+
Vatairea macrocarpa	–	+	–	N.S.	N.S.	–
Seed scarification						
Bowdichia virgilioides	N.S.	+	N.S.	N.S.	N.S.	N.S.
Dimorphandra mollis	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Hymenaea stigonocarpa	–	+	+	–	N.S.	–
Plathymenia reticulata	–	NS	+	–	–	–
Stryphnodendron adstringens	+	+	+	–	N.S.	N.S.
Tachigali rubiginosa	–	+	+	–	–	–

Seed extraction from the fruits negatively affected seedling establishment of larger seeds and positively affected smaller seeds, while seed scarification affected seedling establishment independently of the size (Fig. 5).

Seed and seedling costs

The cost of seed production ranged from \$ 0.002 to 0.257 per propagule (Table 3). The cheapest propagule was a fruit of *Plathymenia*, due to the easy harvest and abundant trees. In contrast, the most expensive propagule was a scarified seed of *Hymenaea*, which needs to be cleaned from the flour pulp and scarified (Table 3). The cost of a seedling 12 months after sowing ranged from US\$ 0.014 for seedlings established from sowing fruits of *Plathymenia* and *Vatairea* to US\$ 1.731 for seedlings established from seeds of *Platypodium*, due to the high costs of seed extraction and low establishment success of this species (Table 3). Seedling cost was 1.6 to 74.6 times higher when fruits were processed for seed extraction. Seedling cost was cheaper when seeds were scarified only in the case of *Dimorphandra* (0.8 times), and varied from 1.3 to 6.0 times higher for all the other species.

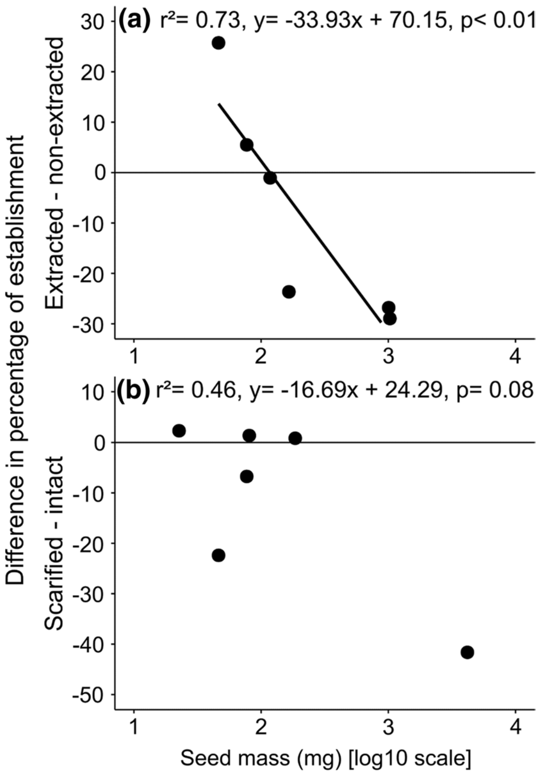

Fig. 5 Relationship of the difference in percentage of seedling establishment in the field for (a) seed extraction treatment (extracted - non-extracted seeds), and (b) seed scarification (scarified - intact seeds), and seed mass (log 10 transformed). Significant linear regression line is shown. Four tree species were submitted to each treatment, and two species were submitted to both treatments. Seeds were sowed in ready-to-seed field environments, and percentage of seedling establishment (number of alive seedlings/number of sowed seeds*100) was calculated

Table 3 Costs of harvesting, seed extraction, seed scarification treatments, and total cost of propagule (sum), proportion of establishment after 12 months (number of established seedlings/number of sowed seeds * 100), and cost of a seedling 12 months after sowing (cost of a propagule/proportion of establishment). Note that seed extraction is also necessary when the propagule is a fruit, for removing impurity, and selecting non-preyed and empty propagules. Cost was calculated in reais (R$) and converted to US$ (R$ 3.93 = US$ 1)

Species/Treatments	Harvesting (US$/unit)	Seed extraction (US$/unit)	Seed scarification (US$/unit)	Unit of planting (US$/unit)	Establishment (%)	1 year old seedling (US$/unit)
Dipteryx alata						
Fruit	0.0338	0.0005	0.0000	0.0344	68.6	0.050
Seed	0.0338	0.0254	0.0000	0.0593	41.1	0.144
Machaerium opacum						
Fruit	0.0027	0.0016	0.0000	0.0043	1.1	0.409
Seed	0.0027	0.0305	0.0000	0.0332	0.0	
Platypodium elegans						
Fruit	0.0043	0.0016	0.0000	0.0059	25.6	0.023
Seed	0.0043	0.0305	0.0000	0.0349	2.0	1.731
Vatairea macrocarpa						
Fruit	0.0046	0.0016	0.0000	0.0062	44.7	0.014
Seed	0.0046	0.0305	0.0000	0.0351	15.5	0.226
Plathymenia reticulata						
Fruit	0.0004	0.0016	0.0000	0.0020	14.1	0.014
Seed	0.0004	0.0191	0.0000	0.0195	39.7	0.049
Broken dormancy seed	0.0004	0.0191	0.0085	0.0280	17.0	0.164
Tachigali rubiginosa						
Fruit	0.0004	0.0016	0.0000	0.0021	1.3	0.163
Seed	0.0004	0.0191	0.0000	0.0195	7.6	0.258
Broken dormancy seed	0.0004	0.0191	0.0085	0.0280	0.0	
Bowdichia virgilioides						
Seed	0.0004	0.0015	0.0000	0.0020	2.5	0.079
Broken dormancy seed	0.0004	0.0015	0.0089	0.0109	4.4	0.249
Dimophandra mollis						
Seed	0.0026	0.0105	0.0000	0.0131	0.8	1.562
Broken dormancy seed	0.0020	0.0105	0.0085	0.0210	1.7	1.249
Hymenaea stigonocarpa						
Seed	0.0125	0.0410	0.0000	0.0535	52.9	0.101
Broken dormancy seed	0.0125	0.0410	0.0106	0.0641	10.5	0.609

Table 3 (continued)

Species/Treatments	Harvesting (US$/unit)	Seed extraction (US$/unit)	Seed scarification (US$/unit)	Unit of planting (US$/unit)	Establishment (%)	1 year old seedling (US$/unit)
Stryphnodendron adstringens						
Seed	0.0018	0.0076	0.0000	0.0094	3.8	0.248
Broken dormancy seed	0.0018	0.0076	0.0085	0.0179	5.6	0.320

Discussion

The literature on tropical trees germination is biased by laboratory studies, while field experiments are rare. Laboratory environments have sufficient and constant soil and air humidity, constant or low-fluctuating temperature, and absence of seed predators. The protocols for seed extraction and dormancy break of tree species aim to accelerate and synchronize germination so that planting stocks for restoration are produced quickly (Koutouan-Kontchoi et al. 2020; Merritt & Dixon 2011). Seed extraction and dormancy break is also recommended (Dayamba et al. 2016) or assumed (Turner et al. 2013; Kildisheva et al. 2020; Passaretti et al. 2020) for successful direct seeding restoration. However, studies testing dormancy break treatments in the field are lacking in the tropics (but see Pereira et al. 2013), and we do not know of studies testing seed extraction.

This study showed that both seed extraction and scarification may reduce emergence under field conditions. Besides, as seed procedures accelerate emergence, they can result in lower seedling survival. After all, the cost of an established seedling (cost of a seed divided by the proportion of seedling establishment) was higher when seeds were extracted from fruits, and when seeds were scarified for all studied species, except for *Dimorphandra*. For this species, higher germination rates could be expected if experiments were longer, reducing or reverting the advantage of scarification. We suggest that, for seasonal tropical savannas and forests, fruit structures and seed coating can protect seeds from extreme variations in temperature and humidity, spread germination over time, and even store moisture to supply the seed in the germination process, becoming devices that increase the success of direct sowing in the field. However, more studies are necessary, by broadening to more regions, different years, population variations in seed dormancy, as evidenced by different results from Pereira et al. (2013). They found that five out of six Cerrado tree species had higher emergence after scarification, resulting in a higher recruitment proportion for three species after one year in the field.

Seed dormancy, and some fruit structures, are adaptive traits for delaying germination for the best timing, and spreading germination to minimize risk in the seasonal tropics (Garwood 1983; Vieira et al. 2008; Ribeiro and Borghetti 2014). This adaptation was most advantageous for seedling emergence and survival in restoration sites. Restoration sites that need whole-site intervention become ready-to-seed, by harrowing or grass-desiccation, which makes them more environmentally stressful than reference sites (Holl 1999; Doust et al. 2006). Added to that, frequent delays in the first rains and dry spells in seasonally dry tropical ecosystems are a major driver of mortality by desiccation of seeds and seedlings (Vieira and Scariot 2006). Besides, direct seeding operations are often conducted well before the best time for germination and seedling establishment, invalidating the assumption that seeding is done at the best time for seedling emergence and survival (Kildisheva et al. 2020). Because ready-to-seed restoration sites are highly temporally and spatially variable, and stressful, seed coating can be used to delay or to bet-hedge seed germination, allowing seeds to await a better time to germinate (Pedrini et al. 2020). Thus, these natural structures, as well as artificial coating and pelleting, are promising for direct seeding in degraded sites. On the other hand, we recognize that in some situations, accelerating and synchronizing seedling emergence are recommended. Fast germination may be advantageous for seeds to escape predation, as well as to make use of the whole rainy season to grow, taking advantage of the weed cover gap after soil preparation (Vieira et al. 2008; Donohue et al. 2010; Grossnickle and Ivetić 2017). Dormancy break treatments are especially important for pioneer species, which have to emerge and quickly cover the ground to outcompete weeds; these species will probably not succeed if they emerge one year after the beginning of the restoration.

As expected, processing and pretreating seeds accelerated and synchronized seedling emergence, but increased seedling mortality during the rainy season due to dry spells or herbivory. Seedling survival was higher when seeds were protected by a robust fruit structure. Such structures seem to retain water and protect the embryo during the germination process, while some extracted seeds died of desiccation or predation by ants, such as *Dipteryx*. Retaining moisture around seeds for longer is one of the functions of seed coating (Turner et al. 2006). That is one of the possible reasons for an emergence increase of 17–55% in broadcast direct seeding for restoration of a sand mining site in the *Banksia* woodlands in Western Australia (Turner et al. 2006). Fruit and seed structures should be studied for these additional properties, such as absorbing and retaining water, and protecting seeds from predation.

In the field, we expected that although processed and treated seeds had lower emergence and early seedling survival, surviving seedlings would be more vigorous and likely to survive during the dry season because they were older than seedlings emerged from unprocessed and untreated seeds. Such expectation was not confirmed. Seedling size (height, diameter, and number of leaves) was not different between treatments at the end of the rainy season (data not shown), possibly because the difference in the time of emergence was no longer than a month, and because the onset of the rainy season has irregular rains that do not allow vigorous seedling growth (Vieira et al. 2008). These findings suggest that for seasonal habitats, it is more advantageous for seeds to germinate when soil moisture is constant than at the very beginning of the rainy season.

We tested sowing seeds within wings or fruit structures for species that had one seed per fruit, or per wing in the case of *Plathymenia*, which has a wing-like papery endocarp carrying a single seed that is dispersed by wind after the fruit opens (Goulart et al. 2005). Species with more than one seed per indehiscent fruit were processed for seed extraction. These multiple-seeded fruits are consumed by animals pre- or post-dispersal (*Dimorphandra*, Bizerril et al. 2005; *H. stignocarpa*, for the same genus see Bello et al. 2017; and *Stryphnodendron*, Kuhlmann 2018b), except for *Bowdichia*, in which three-seeded fruits are wind-dispersed, but probably have secondary seed dispersal, since individual seeds have arils (Albuquerque et al. 2015). Besides, another reason to process multiple-seeded fruits is to avoid loss by sowing numerous seeds at the same spot. These two traits can inform decisions on when to use unprocessed fruits for direct seeding.

Wings or fruit structures enhance seed dispersal but also spread and delay germination. The three samaroid species have a chamber that closely surrounds the seed, which is poorly permeable and penetrable, and have well-closed and cohesive fiber tissues. These species also had higher germination rates in the greenhouse, with optimum and constant soil moisture. Literature is rare and inconclusive on the necessity or advantages of extracting seeds from samaras to enhance the germination of these species. Seeds for restoration are commonly sold with the samaras by the main seed sellers for restoration in Brazil. Extracting these seeds inevitably provokes small injuries to the tegument, which increases mortality by pathogens (Mohamed-Yasseen et al. 1994). Therefore, the samaras of these species can be considered as seed coats, both for nursery seedling production and for direct seeding. The two species that had lower emergence inside the fruit were *Plathymenia* and *Tachigali*. Part of the explanation is that 10 and 15% of the fruits had malformed seeds for *Plathymenia* and *Tachigali*, respectively (data not shown). Another part of the explanation is that many seeds inside the wings were intact up to the end of the experiments, as observed by excavating some seeds, and from other experiments with more extended observations. Thus, a few seeds from these species effectively form seed banks when they are dispersed within their propagules.

Seed scarification altered the germination behavior of the tested species. For species with over-season dormancy, and can emerge in the next rainy season, we verified that scarification increased the proportion of emergence (*Dimorphandra*, *Stryphnodendron*, and *Tachigali*). For the species in which dormancy only spread germination over the first rainy season (within-season germination phenology, sensu Ten Brink et al. 2020), we verified either higher emergence speed (*Hymenaea*) or synchrony (*Bowdichia* and *Hymenaea*). Only *Plathymenia*, a species with fast germination, did not respond significantly to seed scarification in the greenhouse; but it increased its emergence synchrony in the field. Higher and faster seedling emergence can be expected after scarification in the greenhouse for these species, as seen in laboratory conditions (for *Bowdichia* see de Andrade et al. 1997; for *Plathymenia* see Lopes et al. 2010), or even in a greenhouse for *Hymenaea* (Pereira et al. 2013). However, variations in seed lots, seed processing, and in environmental conditions of the greenhouse may have resulted in a weaker dormancy in our experiment. A well spread within-season germination is a trait that causes laboratory protocols to suggest scarification to increase germination in their short-term trials. In any case, results from the laboratory support field procedures when they are the only source of information. In future tests of dormancy breaking for direct seeding, it is important to differentiate within-season phenology from over-season dormancy (Ten Brink et al. 2020). Preserving within-season phenology constitutes a bet hedging strategy for direct seeding (Vieira et al. 2008; Ribeiro and Borghetti 2014). Over-season dormancy might have advantages, such as for late successional species, which benefit from being established under a more closed canopy found one year after direct seeding (Cole et al. 2011), and disadvantages, such as for pioneer species that need full sun to germinate and establish.

One of the major reasons for large seeds to better succeed in direct seeding is that both seeds and seedlings from large-seed species are more resistant to desiccation (Camargo et al. 2002; Tunjai and Elliott 2012; Silva and Vieira 2017; Rodrigues et al. 2019). However, our expectation that the negative effects of seed extraction and scarification in the field would be stronger in smaller seeds was not confirmed. Conversely, seed extraction decreased seedling establishment for larger seeds. Factors such as the small number of tested species, seed-size variation and distribution, and seed-coat type, size and composition contributed to the results. Thus, we consider that testing more species and controlling for seed and fruit traits are necessary to generate conclusive results for this question. Besides seed size, the size of the fruit and particularly of those parts involved in seed protection and water storage may increase seedling-establishment success.

Direct seeding is assumed to be inefficient because seedling emergence and establishment are very low for most species (Ceccon et al. 2016). However, when we compare the cost of an established seedling originated by direct seeding with a nursery grown seedling, it is frequently cheaper, because seeds are extremely cheaper than seedlings (Raupp et al. 2020). Therefore, direct seeding can be more efficient, and further reducing seed costs will have a significant effect on the method's efficiency because they comprise up to 27 to 65% of the cost of the method (Raupp et al. 2020). Seed extraction is a major component of the seed cost. We verified that seed extraction was responsible for 43 to 98% (average 84%) of the seed cost for the species that we studied. Thus, even if a species has higher establishment rates after seed extraction, it should be weighed against the processing cost. Logistics of the seed supply chain also need to be considered in cost-benefit analyses. Such fruit structures are frequently removed for improving purity, storage, seed handling through the seed supply chain, transportation, and fit in mechanical seeders (Urzedo et al. 2016; Smith 2017; Frischie et al. 2020). Another consideration is that seed extraction will become cheaper with technological development and with scalability (Frischie et al. 2020). The seed extraction applied to our studied species are in early technological development, and may become more efficient in the near future.

Seed scarification was responsible for 17 to 82% of the seed cost for the species we studied (average 41%). For only one species out of six, *Dimorphandra*, a 1-year-old seedling was cheaper when seeds were scarified, but this result would change if germination was followed for up to two years, because additional seeds could still germinate. For the other five species, seedling cost was 1.3 to 6.0 times more expensive when seeds were scarified. All species established in the seed extraction treatment had seedling cost 1.6 to 74.6 times more expensive when seeds were processed.

Our findings support a shift in the direct seeding method for the restoration of tropical seasonal forests and savannas. Since savanna restoration must introduce grasses, herbs, and shrubs, future studies should also contribute to improving their seed technology. We suggest that each species or propagule trait has to be tested for seed extraction and dormancy breaking before assuming that processing will be beneficial for increasing emergence and recruitment in direct seeding.

Appendix

See Tables 4 and 5.

Table 4 Results of the statistical analyses for the (i) response variables 'proportion of emergence', 'mean emergence time', and 'synchrony of seedling emergence', for which tested effects were 'species' (six species in each tray), 'seed extraction' (yes or no) or 'seed scarification' (yes or no), and 'environment' (greenhouse or field); and (ii) response variables 'seedling survival' and 'seedling establishment' (number of surviving seedlings /sowed seeds), for which effects tested were 'species' (six species in each tray), 'seed extraction' (yes or no) or 'seed scarification' (yes or no), and 'age' (6 and 12 months). We ran Generalized Linear Models (GLM) for each response variable, with a binomial distribution (logit function) for the counting variables 'seedling emergence', 'seedling survival', and 'seedling establishment', with a gamma distribution for 'mean time of emergence', and with a gaussian distribution for 'emergence synchrony'

Effects	Statistics			
Proportion of emergence (seed extraction)	LR Chi-square	df		*P*
Species (S)	2786.51	5		**< 0.0001**
Seed extraction (SE)	282.23	1		**< 0.0001**
Environment (E)	63.73	1		**< 0.0001**
S*SE	28.60	5		**< 0.0001**
S*E	268.25	5		**< 0.0001**
SE*E	46.01	1		**< 0.0001**
S*SE*E	120.98	5		**< 0.0001**
Proportion of emergence (seed scarification)	LR Chi-square	df		P
Species (S)	2052.49	5		**< 0.0001**
Seed scarification (SS)	12.58	1		**< 0.0001**
Environment (E)	1904.02	1		**< 0.0001**
S*SS	454.39	5		**< 0.0001**
S*E	203.60	5		**< 0.0001**
SS*E	121.54	1		**< 0.0001**
S*SS*E	164.39	5		**< 0.0001**
Mean emergence time (seed extraction)				
Species (S)	743.77	5		**< 0.0001**
Seed extraction (SE)	420.70	1		**< 0.0001**
Environment (E)	65.73	1		**< 0.0001**
S*SE	417.42	5		**< 0.0001**
S*E	26.71	5		**< 0.0001**
SE*E	4.96	1		**0.0260**
S*SE*E	2.63	3		0.4531
Mean emergence time (seed scarification)	LR Chi-square	df		P
Species (S)	1134.26	5		**< 0.0001**
Seed scarification (SS)	479.17	1		**< 0.0001**
Environment (E)	16.99	1		**< 0.0001**
S*SS	239.16	5		**< 0.0001**
S*E	130.74	5		**< 0.0001**
SS*E	1.07	1		0.3008
S*SS*E	14.70	5		**< 0.0001**
Emergence synchrony (seed extraction)	Sum Sq	df	F value	P
Species (S)	0.8608	5	12.7452	**< 0.0001**
Seed extraction (SE)	0.2330	1	17.2487	**< 0.0001**
Environment (E)	0.3888	1	28.7830	**< 0.0001**
S*SE	0.6287	5	9.3090	**< 0.0001**
S*E	0.0813	5	1.2037	0.3178

Table 4 (continued)

Effects	Statistics			
Proportion of emergence (seed extraction)	LR Chi-square	df		*P*
SE*E	0.0132	1	0.9743	0.3274
S*SE*E	0.0903	5	2.2281	0.0936
Residuals	0.8510	63		
Emergence synchrony (seed scarification)	Sum Sq	df	F value	P
Species (S)	0.9124	5	13.4832	**< 0.0001**
Seed scarification (SS)	1.2054	1	89.0702	**< 0.0001**
Environment (E)	0.0090	1	0.6675	0.4168
S*SS	0.8609	5	12.7223	**< 0.0001**
S*E	0.4076	5	6.0233	**< 0.0001**
SS*E	0.0344	1	2.5396	0.1157
S*SS*E	0.2191	5	3.2383	**0.0111**
Residuals	0.9203	68		
Seedling survival (seed extraction)	LR Chi-square	df		P
Species (S)	168.379	5		**< 0.0001**
Seed extraction (SE)	0.009	1		0.9231
Age (A)	0.783	1		0.3762
S*SE	33.194	4		**< 0.0001**
S*A	32.790	5		**< 0.0001**
SE*A	0.055	1		0.8152
S*SE*A	7.963	4		0.0929
Seeedling survival (seed scarification)	LR Chi-square	df		P
Species (S)	62.218	5		**< 0.0001**
Seed scarification (SS)	29.738	1		**< 0.0001**
Age (A)	27.884	1		**< 0.0001**
S*SS	8.144	4		0.0865
S*A	49.127	5		**< 0.0001**
SS*A	2.154	1		0.1422
S*SS*A	11.615	4		**0.0205**
Seedling establishment (seed extraction)	LR Chi-square	df		P
Species (S)	1581.59	5		**< 0.0001**
Seed extraction (SE)	84.53	1		**< 0.0001**
Age (A)	37.10	1		**< 0.0001**
S*SE	734.59	4		**< 0.0001**
S*A	14.45	5		**0.0130**
SE*A	0.02	1		0.8980
S*SE*A	1.22	4		0.8746
Seedling establishment (seed scarification)	LR Chi-square	df		P
Species (S)	1504.41	5		**< 0.0001**
Seed scarification (SS)	217.97	1		**< 0.0001**
Age (A)	97.22	1		**< 0.0001**
S*SS	338.99	4		**<0.0001**
S*A	10.22	5		0.0693
SS*A	0.68	1		0.4081
S*SS*A	1.85	4		0.7629

Table 5 Percentage of seedling emergence at a greenhouse and ready-to-seed field, seedling survival in the field at 6 and 12 months after sowing, and seedling establishment (number of surviving seedlings after 12 months/number of sowed propagules)

Species/Treatments	Emergence seedlings (%)		Field seedling (%)		
	Greenhouse	Field	Survival (Wet Season)	Survival (Dry Season)	Establishment (emerg*surv) 12-mo old
Dipteryx alata					
Fruit	92.00 ± 4.62[a]	75.50 ± 13.53[a]	94.74 ± 1.80[a]	94.53 ± 3.78[a]	67.62 ± 9.54[a]
Seed	55.00 ± 10.52[b]	54.50 ± 3.70[b]	83.79 ± 3.14[b]	89.39 ± 5.17[b]	40.82 ± 2.75[b]
Machaerium opacum					
Fruit	14.00 ± 10.58[a]	7.25 ± 0.96[a]	14.58 ± 3.82[a]	100.00 ± 0.00[a]	1.06 ± 0.58[a]
Seed	0.00 ± 0.00[b]	0.50 ± 0.58[b]	0.00 ± 0.00[b]	0.00 ± 0.00[b]	0.00 ± 0.00[b]
Platypodium elegans					
Fruit	31.00 ± 10.00[a]	35.75 ± 7.93[a]	79.12 ± 4.87[a]	90.07 ± 7.76[a]	25.48 ± 4.86[a]
Seed	9.00 ± 7.57[b]	2.75 ± 1.71[b]	72.50 ± 32.02[a]	91.67 ± 16.67[a]	1.83 ± 0.58[b]
Vatairea macrocarpa					
Fruit	54.00 ± 14.79[a]	53.50 ± 8.85[a]	91.49 ± 2.73[a]	90.92 ± 3.72[a]	44.50 ± 7.72[a]
Seed	0.00 ± 0.00[b]	18.00 ± 12.94[b]	96.88 ± 6.25[a]	89.14 ± 7.60[a]	15.54 ± 11.33[b]
Plathymenia reticulata					
Fruit	69.00 ± 6.83[a]	26.50 ± 9.85[a]	67.40 ± 10.20[a]	77.60 ± 29.64[a]	13.86 ± 7.50[a]
Seed	89.00 ± 5.03[b]	56.50 ± 17.21[b]	80.50 ± 6.24[b]	87.05 ± 8.15[b]	39.59 ± 14.72[b]
Scarified seed	85.00 ± 5.03[b]	32.25 ± 11.18[a]	71.36 ± 2.09[a]	74.75 ± 13.41[a]	17.20 ± 4.20[a]
Tachigali rubiginosa					
Fruit	10.00 ± 5.16[a]	5.00 ± 1.41[a]	63.21 ± 25.51[a]	39.58 ± 25[a]	1.25 ± 1.26[a]
Seed	7.00 ± 6.83[a]	20.25 ± 6.40[b]	74.71 ± 9.24[a]	44.55 ± 25[a]	6.74 ± 5.85[b]
Scarified seed	27.00 ± 16.45[b]	0.50 ± 1.00[c]	00.00 ± 0.00[b]	0.00 ± 0.00[b]	0.00 ± 0.00[c]
Bowdichia virgilioides					
Seed	63.00 ± 6.83[a]	7.00 ± 2.71[a]	46.53 ± 20.93[a]	64.29 ± 47.38[a]	2.09 ± 1.73[a]
Scarified seed	58.00 ± 25.61[a]	9.00 ± 2.71[a]	54.32 ± 27.34[a]	90.28 ± 11.45[a]	4.41 ± 2.22[a]
Dimorphandra mollis					
Seed	8.00 ± 4.62[a]	1.50 ± 1.73[a]	41.67 ± 52.04[a]	100.00 ± 0.00[a]	0.63 ± 0.00[a]
Scarified seed	74.00 ± 10.58[b]	3.50 ± 3.42[a]	41.67 ± 14.43[a]	100.00 ± 0.00[a]	1.46 ± 1.73[a]
Hymenaea stigonocarpa					
Seed	80.00 ± 7.30[a]	74.50 ± 5.45[a]	80.52 ± 8.45[a]	87.04 ± 3.25[a]	52.21 ± 7.27[a]
Scarified seed	82.00 ± 2.31[a]	24.00 ± 8.64[b]	51.18 ± 12.71[b]	86.18 ± 2.49[a]	10.59 ± 5.48[b]
Stryphnodendron adstringens					
Seed	56.00 ± 7.30[a]	7.75 ± 4.35[a]	51.52 ± 26.05[a]	90.63 ± 18.75[a]	3.62 ± 1.71[a]
Scarified seed	85.00 ± 5.03[b]	25.00 ± 15.77[b]	20.50 ± 14.57[b]	97.40 ± 4.44[a]	4.99 ± 4.00[a]

(a) Extracted and non-extracted seeds, and (b) scarified and intact seeds. Four tree species were submitted to each treatment, and two species were submitted to both treatments. The same letters after values indicate no significant difference between extracted and non-extracted seeds, and scarified and intact seeds

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