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Direct seeding reduces costs, but it is not promising for restoring tropical seasonal forests

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ABSTRACT

Direct seeding is a potential technique to restore forests; however, further studies are needed before its application on a large scale. We carried out a field experiment in a deforested area in southern Brazil to test the technical and economic feasibility of a direct seeding system with high tree species diversity to restore the tropical seasonal forest. We also compared species performances and tested the effects of seed size and successional group on tree seedling emergence and development. The trial was established at two different sowing times using 31 tree species. For two years after sowing we evaluated seedling emergence, establishment, survival and early growth of tree species, weed competition and costs for plantation establishment and early maintenance. Most species had low seedling emergence and establishment, but high survival rates, implying that low seedling emergence is the main barrier to community assembly that must be overcome. The most successful species had larger seeds, belonged to non-pioneer categories and had slower growth rates. Final costs after two years were lower than has been reported in the literature for most restoration planting using seedlings both in Brazil and elsewhere; however, seedling density was low. Although direct seeding may be a feasible alternative to decrease planting costs, the poor species performances and low seedling density may reduce its applicability. Thus, we recommend direct seeding only in association with the planting of pioneer species seedlings.

1. Introduction

Most methods of tropical forest restoration use high diversity plantings of nursery-raised seedlings, which has been the predominant approach in Brazil (Durigan et al., 2013; Rodrigues et al., 2009a; Sampaio et al., 2007) and many other tropical regions (Lamb et al., 2005). However, in many circumstances these approaches are too costly to be adopted at the large scales needed (Lamb et al., 2005). Techniques are required that kick-start natural succession and ecosystem development at a low cost and with minimal inputs, to ensure ecosystem resilience and stability, providing direct benefits for mankind (Engel and Parrotta, 2008).

A possible pathway to ecological restoration is the direct seeding technique, where seeds of forest species are sown directly on the site, instead of being outplanted as nursery-raised seedlings (Birkedal, 2010; Cole et al., 2011). Direct seeding has been considered a simple, convenient and inexpensive technique that is easily adopted by the owners of small and medium-sized plots (Camargo et al., 2002; Ceccon et al., 2016; Douglas et al., 2007; Engel and Parrotta, 2001; Knight et al., 1998). Nevertheless, many factors will affect the efficacy of the method, such as species and seed characteristics and environmental conditions (Doust et al., 2008; St-Denis et al., 2013; Wang et al., 2011). It is still necessary to improve its efficiency, applicability and effectiveness (Hossain et al., 2014; Pereira et al., 2013; St-Denis et al., 2013).

Many studies have been undertaken to investigate the success of direct seeding in the restoration of abandoned fields (Dodd and Power, 2007; Hooper et al., 2002; St-Denis et al., 2013). Considering that tree species richness of tropical forests is very high, the selection of the right species is essential to ensure that direct seeding can be applied effectively (Tunjai and Elliott, 2012). Furthermore, the lack of information on costs may limit the application of direct seeding systems on a broader scale. To date, only a few studies have analyzed direct seeding implantation and maintenance costs, and all of these focused on systems established with relatively low species richness (Cole et al., 2011; Douglas et al., 2007; Engel and Parrotta, 2001).

This paper investigates the technical and economic feasibility of a manual direct seeding system with high tree species diversity to restore the tropical seasonal forest in southeastern Brazil. We addressed the following questions: a) Is it possible to achieve high seedling density and species diversity using direct seeding? b) Are direct seeding methods more cost-effective than planting nursery-raised seedlings? c) Do seed size and successional group affect seedling emergence,

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Table 1
Soil chemical attributes of the study site (0–20 cm depth).

Depth (cm)	pH	O.M.[a]	Pextractable	H + Al	K	Ca	Mg	BS[b]	CEC[c]	V%[d]
	CaCl2	g/dm^3	mg/dm^3	mmolc/dm^3						
0–5	5.4	35	8	14	2.0	17	7	26	40	65
5–10	5.0	23	6	15	1.4	14	4	19	34	57
10–20	4.7	20	4	17	1.1	11	4	16	33	49

[a] Organic matter.
[b] Base sum.
[c] Cation exchange capacity.
[d] Base saturation.

establishment, survival and growth? d) How do the native species sowed differ in their field performance and which are most suited for direct seeding projects in the region?

2. Materials and methods

2.1. Study site

A direct seeding trial was established in an abandoned pasture located on a property within the campus of the São Paulo State University (UNESP) at Botucatu municipality, in the south-central region of the state of São Paulo (22°50′S; 48°24′W), Brazil. The site was dominated by invasive exotic grasses, mainly *Urochloa decumbens* (Stapf.) Webster and *Panicum maximum* Jacq. (Poaceae), and was situated next to a secondary forest fragment, which was classified as seasonal, semi-deciduous, tropical forest.

The soil is a moderately acidic and leached, sandy Oxisols of very low fertility (Table 1) and prone to severe laminar erosion. The average annual rainfall is 1494 mm, concentrated between October and March (Fig. 1). The mean annual temperature is 20.5 °C, with the minimum average occurring in July and maximum in February (Nogueira Júnior et al., 2011). The local topography is moderately hilly, with elevations ranging from 464 to 775 m.

2.2. Site preparation, maintenance and experimental design

The experiment was established at two different sowing times, January (first sowing time) and November (second sowing time) of 2009. The experimental trial had four replicates (80 m × 20 m), resulting in a total experimental area of 0.64 ha. Each sowing had a different range of species; the first sowing used 14 native forest species and the second one used 17 (Table 2).

The site was prepared one month before the first sowing with one mechanical application of post-emergence, non-residual herbicide (Roundup Original® 5.0 L.ha^{-1}, with the active ingredient glyphosate). After two weeks, the desiccated straw was mown and the sowing lines were prepared using a ripper pulled by a tractor, with 2 m spacing between lines.

For the first sowing time, the seeds were buried in spots manually along the planting lines, with 1 m spacing between spots (three seeds of the same species per spot). For the second sowing time, the seeds were placed evenly in the spots left by the first sowing germination failures. For both sowing times, the sowing depth was approximately 5–20 mm, depending on seed size. No thinning was carried out in cases where more than one seed germinated per spot in order to allow intraspecific competition and natural selection to operate.

The species were grouped into two broad classes: pioneers (typical of early succession phases, fast-growing trees with short lifespans, light-demanding seedlings, small and dormant or orthodox seeds) and non-pioneers (late secondary and climax species, mid to slow-growing trees with longer lifespans, shade-tolerant seedlings, larger and non-dormant or recalcitrant seeds), based on information from the literature (Martins et al., 2009; Silva et al., 2004) and personal observations. In each line, we sowed species belonging to only one group, in this way we had 10 lines per replicate: 5 with pioneer species and 5 with non-pioneer species. The species sequence in each line was randomized and this same sequence was repeated in all lines.

After sowing, weed control consisted of three manual applications per year (beginning and end of wet season and middle of dry season) of post-emergence, non-residual herbicide (Roundup Original® 5.0 L.ha^{-1}, active ingredient glyphosate), to ensure seedling survival and good early growth. During herbicide application, the seedlings were protected with polyethylene containers. Furthermore, ant traps containing formicide (Mirex-S® active ingredient sulfluramid) were set up at selected spots between the lines twice a year (according to visual ant presence) to reduce seed and seedling predation. The weed and ant control was carried out for two years after the first sowing; no further weed or ant control was applied after that period.

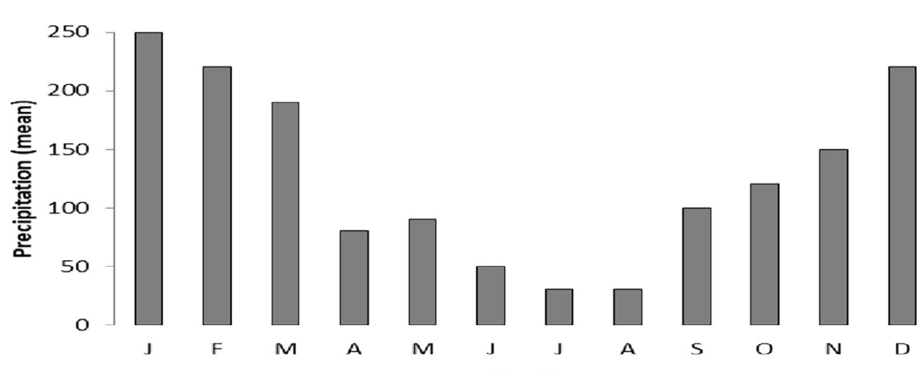

Fig. 1. Monthly precipitation in the study site. Mean precipitation measured from 1971 to 2013 at the Weather Station installed within the campus of the São Paulo State University (UNESP) at Botucatu (22°50′S; 48°25′W). Available on http://estacaolageado.fca.unesp.br/index.html. Accessed December 18, 2017.

Table 2
List of study sites, sowing time, successional group, seed sizes and potential germination rate estimated in the nursery.

Species[a]	Family	Sowing time[b]	Successional group[c]	Seed size[d]	GR (%)[e]
Allophylus edulis (A. St.-Hil., Cambess. and A. Juss.) Radlk	Sapindaceae	F	NP	S	–
Amburana cearensis (Allemão) A.C. Sm.	Fabaceae (Faboideae)	S	NP	M	0
Anadenanthera falcata (Benth.) Speg.	Fabaceae (Mimosoideae)	S	P	M	67
Aspidosperma polyneuron Müll. Arg.	Apocynaceae	S	NP	M	50
Aspidosperma ramiflorum Müll. Arg.	Apocynaceae	S	NP	M	100
Bauhinia forficata Link	Fabaceae (Cercideae)	S	NP	M	67
Citharexylum myrianthum Cham.	Verbenaceae	F	P	S	–
Copaifera langsdorffii Desf.	Fabaceae (Caesalpinioideae)	F	NP	L	–
Cordia trichotoma (Vell.) Arráb. Ex Steud.	Boraginaceae	S	P	S	0
Croton floribundus Spreng.	Euphorbiaceae	F	P	S	–
Eugenia uniflora L.	Myrtaceae	S	NP	L	33
Eugenia pyriformis Cambess.	Myrtaceae	S	NP	L	33
Genipa americana L.	Rubiaceae	F	P	S	–
Guarea guidonia (L.) Sleumer	Meliaceae	F	NP	M	–
Handroanthus chrysotrichus (Mart. ex A. DC.) Mattos	Bignoniaceae	S	P	S	50
Hymenaea courbaril var. *stilbocarpa* (Hayne) Y.T. Lee and Langenh.	Fabaceae (Caesalpinioideae)	F	NP	L	–
Inga vera subsp. *affinis* (DC.) T.D. Penn	Fabaceae (Mimosoideae)	F	P	L	–
Machaerium acutifolium Vog.	Fabaceae (Faboideae)	S	P	M	20
Mimosa bimucronata (DC.) O. Kuntze	Fabaceae (Mimosoideae)	S	P	S	0
Myroxylon peruiferum L. f.	Fabaceae (Faboideae)	S	NP	L	60
Nectandra megapotamica (Spreng.) Mez	Lauraceae	F	NP	M	–
Ormosia arborea (Vell.) Harms	Fabaceae (Faboideae)	F	NP	L	–
Parapiptadenia rigida (Benth.) Brenan	Fabaceae (Mimosoideae)	S	P	S	77
Peltophorum dubium (Spreng.) Taub.	Fabaceae (Caesalpinioideae)	S	P	S	73
Platypodium elegans Vogel	Fabaceae (Faboideae)	F	P	L	–
Pterocarpus violaceus Vogel	Fabaceae (Faboideae)	S	NP	L	33
Pterogyne nitens Tul.	Fabaceae (Caesalpinioideae)	S	P	M	23
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	F	NP	S	–
Rapanea gardneriana (A. DC.) Mez	Myrsinaceae	F	P	S	–
Schinus terebinthifolius Raddi	Anacardiaceae	F	P	S	–
Zeyheria tuberculosa (Vell.) Bureau	Bignoniaceae	S	P	M	0

[a] Nomenclature follows that of Lorenzi (2008).
[b] Sowing time: F (First sowing), S (Second sowing).
[c] Successional group: P (pioneer), NP (non-pioneer).
[d] Seed size category based on seed weight: S = Small (< 0.069 g), M = Medium (0.07–0.39 g), L = Large (greater than 0.40 g).
[e] GR: Potential germination rate estimated in nursery trials (defined as the percentage of germinated seeds per number of seeds sown).

2.3. Tree species selection, seed collection, storage and pre-germination treatments

Species were selected based on their ecophysiological and silvicultural characteristics, including fecundity, fruiting period and the availability of seeds in the period just before our experiment, based on Lorenzi (1998, 2008) and Carvalho (2003). Thirty-one species from 14 families were chosen, representing different successional groups and including a wide range of seed sizes, germination requirements, growth forms and dispersal mechanisms (Table 2).

The seeds were collected during the three months prior to sowing, from at least three parent trees in natural forests around the experimental site to adequately represent the gene pool of wild populations and to ensure their adaptability to the study site conditions. After collection, seeds were removed from pods and stored in a cold chamber until the sowing time. Pre-germination treatments were carried out for 12 out of the 31 species, according to recommendations in the literature (Floriano, 2004; Fowler and Bianchetti, 2000).

For the first sowing period, no prior seed viability test was performed, and seeds were chosen by visual inspection. For the second sowing time, seed germination tests were performed in the same week as the field trial installation. Seeds were sown in polyethylene trays filled with sterilized sand, with three replicates and a variable number of seeds per species (according to their sizes), and were placed in a tree nursery. Trays were split into four sections, where each one received a different species. The trays were watered regularly and submitted to natural conditions for seed germination. The dormant seeds were previously subjected to the same pre-germination treatments as the seeds for the field trials. We counted the number of emerged seedlings weekly for three months. The results of these tests are summarized in Table 2.

2.4. Data collection and statistical analysis

The experiment was monitored two years after the first sowing. To assess the species performances and seedling density, we recorded the proportion of seeds that germinated and survived as seedlings (defined as the percentage of live seedlings per number of seeds sown) monthly for the first six months after each sowing and then at three-month intervals up to two years after the first sowing. Emergence and establishment were defined as the percentage of live seedlings at six and 12 months after sowing, respectively. Seedling height (defined as the distance between the soil surface and the tip of the seedling's terminal axis) and survival (number of live seedlings as a percentage of the number of germinated seeds in the first year after sowing, and as a percentage of the number of established seedlings in the second year after sowing) was recorded at 12 and 24 months following the first sowing and 12 months following the second sowing, for each species. The suitability of the species for direct seeding was defined according to their mean establishment rate: suitable species (10% or more), non-suitable species (< 10%) and failed species (species not established at all).

To verify whether seed size and successional group affect seedling emergence, establishment, survival and height for tested species, we performed analyses of variance (ANOVA) and *post hoc* comparisons for pair-wise comparisons of means using Tukey's HSD test ($\alpha = 0.05$). Variables expressed as a percentage (emergence, establishment and survival) were transformed by a square root function before analysis in order to meet assumptions of normality and homogeneity of variances. All statistical tests were performed with Assistat 7.5 Beta Software (Universidade Federal de Campina Grande, Brazil). For all tests, failed species (species that did not germinate at all) were not considered.

To evaluate weed infestation, the percentage cover of weeds was assessed six and 12 months after the first sowing by a visual estimate from eight randomly selected 50 × 50 cm quadrats placed flat on the ground within the area. The soil coverage was divided into three groups: no weed coverage, exotic grasses (*U. decumbens* and *P. maximum*) and other weed species.

To verify the economic feasibility of direct seeding method we computed all establishment (purchase of seeds, soil preparation and sowing) and maintenance (ant and weed control) costs for the two years after the first sowing, then, we compared our results to those found in the literature for planting nursery-raised seedlings in the study region. The costs of labor and supplies were based on data presented by Instituto de Economia Agrìcola (2011) for the region, and the machinery and equipment costs were based on Agrianual (2010) for reforestation purposes. The cost of purchasing the seeds was estimated by surveying several nurseries and seed suppliers; the lowest price found for each species was used. The number of seeds.kg^{-1} was based on Lorenzi (2008).

3. Results

3.1. Seedling emergence, establishment and growth rates

The potential germination rate estimated in the nursery for the 17 species used in the second sowing was at least 50% for eight species, which showed that in general the seeds had good viability (Table 2), so low seed vigor was not considered as a reason for low germination in the field for most species. Only four species did not germinate in the nursery and, of these, three did not germinate either in the nursery or in the field, implying that their seeds were not viable.

Emergence, establishment and height of species varied greatly. Seeds of 24 species out of 31 germinated in the field, and only four did not establish seedlings until one year after sowing. However, seedling emergence and establishment were very low for most species. Of the 31 species tested, only 10 had emergence rates higher than 10%, and among them, only six had establishment rates higher than 10% (Table 3).

Although emergence and establishment were low for most species, survival was generally high for most species that germinated. Of the 24 species that emerged, 12 had survival rates higher than 60% up to one year after sowing. Among the 12 established species from the first sowing, eight had survival rates higher than 60% up to two years after sowing.

Seedling growth was very low for most species in the first year after sowing. Seedling height varied from 9.5 to 83.5 cm, and the average height was greater than 50.0 cm only for four species. In the second year after sowing, only three species had an average height greater than or equal to 100.0 cm (Table 3).

3.2. Influence of seed size and successional groups on seedling emergence and early development

Seedling emergence and establishment varied significantly among seed size categories and successional groups. Emergence and establishment were higher in species with larger seeds (emergence: $F = 48.21$, $df = 2$, $p < 0.0001$; establishment: $F = 21.75$, $df = 2$, $p = 0.0006$) and species within the non-pioneer group (emergence: $F = 12.76$, $df = 1$, $p = 0.0119$; establishment: $F = 6.98$, $df = 1$, $p = 0.0375$).

Seed size also affected survival rates in the first year after sowing ($F = 14.39$, $df = 2$, $p = 0.0020$), whereby species with larger seeds had higher survival rates. However, seed size had no effect on survival rates in the second year after sowing ($F = 1.04$, $df = 2$, $p = 0.3952$), and successional group also had no effect on survival rate after either the two time periods (Survival at 1 year: $F = 0.13$, $df = 1$, $p = 0.9100$; Survival at 2 years: $F = 0.74$, $df = 1$, $p = 0.5733$).

Seedling growth was significantly affected by seed size (height at 1 year: $F = 5.51$, $df = 2$, $p = 0.0271$; height at 2 years: $F = 25.60$, $df = 2$, $p = 0.0004$) and successional group after both time periods (height at 1 year: $F = 20.25$, $df = 1$, $p = 0.0046$; height at 2 years: $F = 198.84$, $df = 1$, $p < 0.0001$). Species with larger seeds had lower growth rates and, as expected, pioneer species had higher growth rates (Figs. 2 and 3).

3.3. Seedling density

Emergence and establishment were generally low for all species, resulting in comparatively low seedling density relative to the density of seeds sown. The final density was 1265 surviving seedlings.ha^{-1} up to two years after the first sowing. The first sowing contributed to 497 surviving seedlings.ha^{-1} and the second one to 768 surviving seedlings.ha^{-1}.

3.4. Weed competition

The percentage of soil covered by weeds was 69% at the end of the wet season (46% by exotic grasses and 23% by other weeds) and 61% at the beginning of the wet season (29% by exotic grasses and 31% by other weeds). This high weed infestation occurred all year round. However, as expected, it was higher at the end of wet season, mainly for exotic grasses, since the water availability was higher during this period, allowing quick recovery.

3.5. Costs

The total cost of seed purchase was US$ 205.20, which represented 26.4% and 11.2% of the establishment and total costs, respectively. The species used in the first sowing had prices 33.4% lower than those used in the second sowing, demonstrating that the choice of species affects the total cost of direct seeding. However, the main factor that increased the final cost was post-seeding weed control, which represented 50.1% of the total costs (Table 4).

4. Discussion

4.1. Suitability groups

4.1.1. Group 1 – Suitable species

Species allotted to this group were the most suited to direct seeding techniques because of their higher establishment rates (meaning that less seeds need to be sown). Only six out of 31 species tested fell into this group: *Eugenia pyriformis*, *Hymenaea courbaril*, *Platypodium elegans*, *Eugenia uniflora*, *Inga vera* and *Bauhinia forficata*. In addition to their higher establishment, all species had high survival rates, even when weed competition was high. These characteristics might be explained by the size of their seeds. All six species had medium to large seeds, which contain more resources and result in more vigorous seedlings, meaning that they can resist field conditions (Camargo et al., 2002). However, in general they also have very slow growth. *E. pyriformis* and *E. uniflora* were, on average, only 10–20 cm in height one year after sowing (Table 3), which can reduce their chances of establishment in the long term. In addition, their seeds are recalcitrant with high water content when dispersed, which may compromise the seeds' viability in storage conditions (Kaiser et al., 2014) and their use in direct seeding systems. On the other hand, *P. elegans* seemed to be more suitable for direct seeding systems. The seedling height one year after sowing was over 30 cm, which was, on average, almost twice the height of *Eugenia* spp. seedlings. Araki (2005) also reported good establishment and growth rates for *P. elegans* in his experiment.

B. forficata and *H. courbaril* are considered non-pioneer species, although they had rapid growth, which can be explained by their seed size. Cartaxo (2009) and Ferreira et al. (2009) also described the good

Table 3
Suitability group classification; percentage of seedling emergence, establishment, survival and height; costs/1000 seeds.

Group	Species	Emergence,% (+ S.E.)	Establishment,% (+ S.E.)	Survival,% (+ S.E.)		Height, cm (+ S.E.)		Costs/1000seeds, US$
				1 year	2 years	1 year	2 years	
Suitable species	*E. pyriformis*	34.2 (2.7)	24.1 (7.6)	70.5 (24.2)	–	13.8 (2.1)	–	31,42
	H. courbaril	27.7 (8.7)	22.7 (4.2)	81.9 (14.4)	69.4 (32.7)	44.5 (4.5)	80.2 (14.7)	12,72
	P. elegans	29.9 (6.2)	20.8 (9.7)	69.4 (21.9)	70.1 (21.6)	38.8 (10.8)	69.1 (22.7)	13,77
	E. uniflora	27.4 (12.2)	17.3 (6.1)	63.2 (5.7)	–	16.5 (3.0)	–	9,93
	I. vera	27.9 (9.2)	11.4 (2.7)	41.1 (16.6)	87.1 (17.3)	50.6 (10.3)	100.0 (11.3)	6,97
	B. forficata	12.3 (5.7)	11.4 (10.1)	92.9 (36.6)	–	48.2 (26.3)	–	1,76
Non-suitable species	*M. peruiferum*	12.8	9.3	72.9	–	15.5	–	33,68
	C. langsdorffii	12.2 (4.5)	7.9 (3.4)	64.9 (24.0)	72.3 (27.3)	18.1 (3.3)	39.0 (10.7)	9,25
	C. floribundus	9.6 (2.7)	6.4 (2.6)	67.0 (30.1)	51.6 (45.0)	83.2 (35.0)	247.1 (23.6)	3,09
	N. megapotamica	12.4 (4.9)	3.7 (4.9)	30.3 (28.1)	100.0 (17.3)	28.8 (10.6)	50.5 (6.4)	20,15
	P. dubium	3.4 (4.3)	2.9 (3.3)	85.0 (25.1)	–	50.3 (13.8)	–	3,99
	O. arborea	13.2 (6.0)	2.7 (1.7)	20.9 (14.8)	62.7 (5.7)	16.0 (2.8)	33.3 (11.5)	13,25
	P. violaceus	4.1 (4.2)	2.6 (3.0)	62.5 (25.5)	–	9.5 (4.9)	–	46,09
	A. falcata	0.3 (0.7)	2.0 (4.2)	100.0 (0.0)	–	25.0 (0.0)	–	22,65
	C. myrianthum	6.1 (5.8)	0.7 (1.1)	11.3 (11.0)	100.0 (0.3)	49.7 (15.0)	78.7 (12.4)	3,85
	M. acutifolium	1.0 (1.3)	0.6 (0.8)	66.6 (35.4)	–	11.0 (2.1)	–	3,79
	P. rígida	2.9 (2.8)	0.6 (1.4)	23.5 (50.0)	–	35.0 (0.00)	–	2,01
	S. terebinthifolius	3.1 (0.7)	0.6 (0.8)	22.1 (6.4)	100.0 (28.8)	67.0 (6.4)	140.0 (28.3)	1,94
	A. polyneuron	2.0 (2.9)	0.5 (1.0)	25.0 (0.0)	–	23.0 (0.0)	–	6,97
	A. edulis	4.1 (2.6)	0.4 (0.8)	10.1 (0.0)	0.1 (0.0)	41.3 (0.0)	–	0,36
Failed species	*G. Americana*	2.0 (3.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	–	–	0,74
	G. Guidonia	2.8 (2.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	–	–	27,12
	H. chrysotrichus	1.0 (2.1)	0.0 (0.0)	0.0 (0.0)	–	–	–	1,35
	P. nitens	1.0 (2.1)	0.0 (0.0)	0.0 (0.0)	–	–	–	8,93
–	*A. cearenses*	–	–	–	–	–	–	48,84
	A. ramiflorum	–	–	–	–	–	–	23,94
	C. trichotoma	–	–	–	–	–	–	2,59
	M. bimucronata	–	–	–	–	–	–	11,88
	P. heptaphyllum	–	–	–	–	–	–	0,96
	R. gardneriana	–	–	–	–	–	–	1,24
	Z. tuberculosa	–	–	–	–	–	–	4,95

performance of *B. forficata* and *H. courbaril* in their direct seeding experiments, respectively. However, further studies are needed to evaluate whether this good performance persists over time or is restricted to early establishment only.

Although *I. vera* performed well in our study, its seeds have high water content, are extremely recalcitrant and are only available for a very limited period during the year. To date there is no protocol to safely dry or store seeds of this species (Faria, 2006), which may hinder its use on a large scale.

4.1.2. Group 2 – Non-suitable species

Species allotted to this group are not suited to direct seeding techniques due to their low seedling emergence and establishment. Most species that fell into this group were pioneers with small seeds (Table 3). Although they had low establishment, their growth rates were very high, which is an essential feature in guaranteeing their success in direct seeding conditions. Thus, to overcome their poor performance it may be necessary to increase the density of seeds sown in the field. Moreover, since weed competition was probably one of the main factors that led to their poor establishment rates, choosing species that can overcome this barrier may increase final seedling density.

4.1.3. Group 3 – Failed species

Species allotted to this group had very low emergence rates (< 2%) and no surviving seedlings following the first year after sowing. Four species fell into this group: *G. americana*, *G. guidonia*, *H. chrysotrichus* and *P. nitens* (Table 3). All of these species had small to medium seeds, illustrating the high impact of this characteristic on species performance. The seeds of *G. guidonia* and *G. americana* have high moisture content and lose viability quickly when stored (Conserva et al., 2013; Queiroz et al., 2012), which may explain their poor performances. On the other hand, seeds of *H. chrysotrichus* and *P. nitens* were tested in the nursery and showed emergence rates over 20%; thus, they had good viability in nursery conditions but not in the field. Certainly, ecological filters in the experimental field constrained their emergence. Further studies must assess these filters and how to overcome them.

4.2. Effect of seed size on seedling emergence and early development

Many studies have indicated that species with larger seeds have an advantage in germination and early establishment (Ceccon et al., 2016; Hossain et al., 2014; Pereira et al., 2013; Tunjai and Elliot, 2012; Wang et al., 2011). Our results are in accordance with this: species with larger seeds had higher germination, establishment and survival rates in the first year after sowing. The advantage of larger seeds might be explained by their higher tolerance to stressful conditions during early establishment, since they contain more reserves (Baskin and Baskin, 1998; St-Denis et al., 2013; Tunjai and Elliot, 2012). Moreover, in general, species with small seeds produce seedlings that are more susceptible to negative environmental conditions and do not resist long periods of adversity (Camargo et al., 2002). However, there was no significant effect on survival rate up to two years after sowing, implying that this effect occurred only during early establishment.

On the other hand, there was a negative effect of seed size on seedling growth rates. Species with smaller seeds had faster growth, which may be explained by the fact that they were mainly pioneers.

4.3. Effects of successional group on seedling emergence and early development

Among the species tested, non-pioneers had some advantages over pioneers. Non-pioneers had higher seedling emergence and

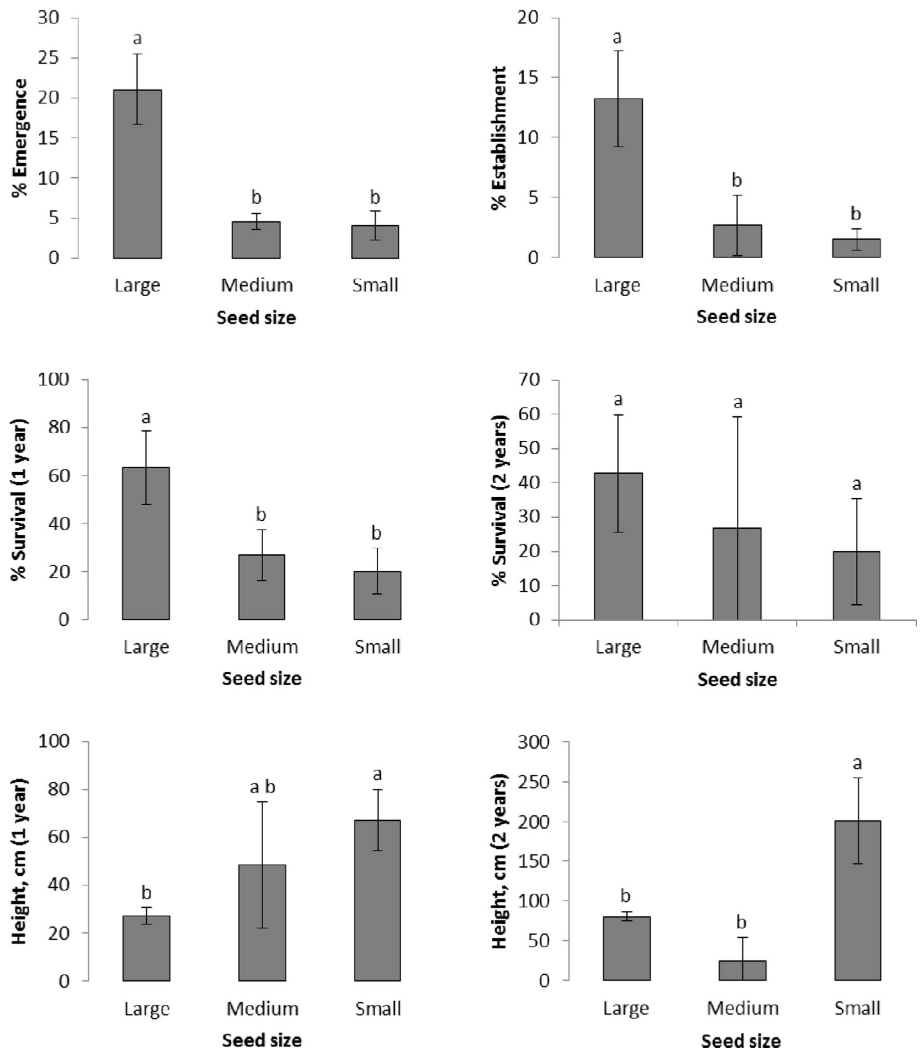

Fig. 2. The effect of seed size on seedling emergence, establishment, survival and growth. Vertical bars are mean ± SE. Means followed by the same letters do not differ at 5% level (Tukey's HSD at α = 0.05).

establishment rates, which is a result also demonstrated by Knowles and Parrotta (1995) and Camargo et al. (2002) in their direct seeding experiments. Seeds of pioneers require special environmental conditions for dormancy break and/or germination, so seed reserves may be depleted before these conditions are created (Baskin and Baskin 1998). Moreover, pioneer species have less vigorous seedlings, which may have decreased the establishment rate or even resulted in an underestimation of the germination rate, if seeds germinated but then died between observations.

As expected, non-pioneer species had slower growth, which is not a desirable characteristic for species used in direct seeding systems (Doust et al., 2008), as it is intended to cover the ground rapidly in order to overcome weed competition. On the other hand, successional group did not significantly affect survival rate for either sowing time, which is different to previous studies (Camargo et al., 2002), where non-pioneers had higher survival rates.

4.4. Weed competition

Weeds recovered quickly after both sowings. Therefore, it was necessary to implement several weeding procedures, since the grasses were growing on spots (which could prevent germination by creating a physical barrier) and on emerged seedlings (which could inhibit the growth and survival of seedlings) (D'Antonio and Meyerson, 2002; Pereira et al., 2013; Sun et al., 1995; Willoughby and Jinks, 2009). Thus, weeding was the most important maintenance activity to ensure the native seedlings' survival, particularly during the wet season.

Despite all the control measures adopted, one of the main factors that may have contributed to poor seedling performance was the infestation of the site with exotic, invasive grasses. Careful weeding before sowing and during the first year of establishment is essential to reduce seedling mortality and increase the chance of direct seeding success (Douglas et al., 2007; Knight et al., 1998; Willoughby and Jinks, 2009). Moreover, weed control in directly sown sites is more difficult than in areas planted with seedlings because of the irregular spacing and reduced size of seedlings (Douglas et al., 2007).

Two of the main criteria in selecting species for direct seeding systems are quick germination and fast early growth rates (Douglas et al., 2007; Doust et al., 2008) in order to compete with exotic grass species and to create soil coverage that prevents future weed germination. However, in our project the species with better performances were in general non-pioneers, which had larger seeds. These species had slow growth rates, so they are not useful in overcoming the weed competition barrier, restricting their use in these conditions. The main weed species that colonized the experimental area were exotic grasses (mainly *U. decumbens* and *P. maximum*), which are considered one of the most problematic factors for seedling development because of their aggressiveness in the field (Sun et al., 1995). They are exceptional competitors, and within a few months of seeding they had colonized the area and interfered with seedling emergence, survival and growth rates.

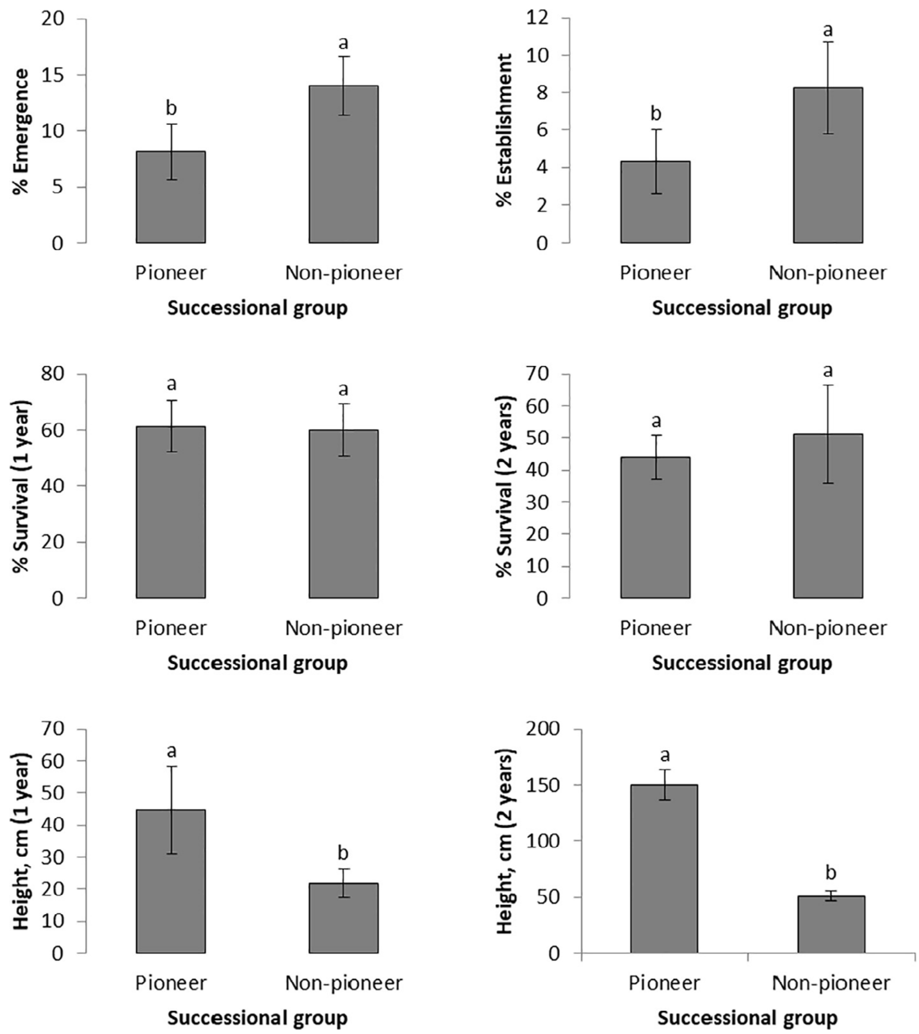

Fig. 3. The effect of successional group on seedling emergence, establishment, survival and growth. Vertical bars are mean ± SE. Means followed by the same letters do not differ at 5% level (Tukey's HSD at $\alpha = 0.05$).

Weed competition may have contributed more to the low germination after the second sowing time. After the first sowing time the emerged seedlings experienced lower weed competition for a longer initial period, because precipitation decreased, resulting in reduced weed infestation. On the other hand, the emerged seedlings from the second sowing had to face higher weed infestation just after germination, when they were not yet able to compete. Studies showed that a later sowing time might be preferable to avoid serious weed competition, since sowing time can influence weed re-establishment and subsequently can affect the extent and timing of competition endured by the sown seedlings (Doust et al., 2008). Our study did not aim to compare different sowing times, since we used a different pool of species in each one, in order to achieve higher species richness. So, future studies using the same species in both sowing seasons are needed to allow direct comparisons to be made and to properly understand this potential pattern.

4.5. Costs

The final costs were lower than those reported in the literature for the majority of restoration systems using seedlings, both in Brazil and elsewhere. Although low-input plantations by nursery-raised seedlings can cost from US$ 1200 to 2500.ha^{-1} (Engel and Parrotta, 2001). Brancalion et al. (2010) reported costs varying from US$ 3181 to 5302 for establishment plus maintenance for two years in forest restoration projects aiming at an average plant density of 1667 individuals.ha^{-1}. Rodrigues et al. (2009b) reported establishment and initial maintenance costs of forest restoration projects with native species (3.0 m × 2.0 m spacing) of around US$ 4683, of which US$ 3669 was for establishment, US$ 595 for maintenance in the first year and US$ 418 in the second year, for an expected tree density of 1667 individuals.ha^{-1}.

Other studies on direct seeding have reported lower costs. For the manual sowing of five species the costs ranged from US$ 742 to 912.ha^{-1} (Engel and Parrotta, 2001) in the first two years (establishment plus maintenance). For a mechanized direct seeding system with eleven species, the establishment costs ranged from US$ 297 to440.ha^{-1} (Engel et al., 2002).

Seedling purchase can represent 55% (Toledo and Mattos, 2008) to 70% (Nascimento, 2007) of forest restoration project costs for abandoned areas in the first year after planting (establishment and maintenance), for a density of 1667 individuals.ha^{-1}. In our study, seed purchase represented 16% of total costs in the first year after seeding (establishment and maintenance) and the seed prices varied widely among species. However, several species that had costly seeds also had low emergence and establishment in the field, so there would be no reason to use them in future projects under the same conditions. Thus, one strategy to reduce costs would be to use a more restricted species pool and to choose only the most adapted ones (species with higher germination and survival rates in the field). This strategy would

Table 4
Establishment and maintenance costs for direct seeding for the first two years of study[a].

	Operations and inputs	Costs (US$.ha^{-1})
Establishment costs	Mechanical herbicide application[b,c]	65.71
	Herbicide[i]	24.95
	Mechanical mowing[b,d]	43.81
	Subsoiling[b,e]	56.89
	Manual seeding (first sowing)[f]	190.92
	Seeds (first sowing)	82.05
	Manual seeding (second sowing)[f]	190.92
	Seeds (second sowing)	123.15
	Subtotal	778.40
Maintenance costs (year 1)	Manual herbicide application[g]	381.84
	Herbicide[i]	74.85
	Formicide application[h]	31.82
	Formicide[j]	33.34
	Subtotal	521.85
Maintenance costs (year 2)	Manual herbicide application[g]	381.84
	Herbicide[i]	74.85
	Formicide application[h]	31.82
	Formicide[j]	33.34
	Subtotal	521.85
	Total costs	1,822.10

[a] During the period of study 1 US$ = 1886 BRL; labor costs averaged US$ 15.91 per 8-h working day.
[b] Including machinery and labor costs.
[c] Machine cost.day^{-1} = US$ 49.80.
[d] Machine cost.day^{-1} = US$ 27.89.
[e] Machine cost.day^{-1} = US$ 40.97.
[f] Three employees for four days.
[g] Two employees for four days.
[h] One employee for one day.
[i] Herbicide cost = US$ 24.95 per 5 L (5l ha^{-1}).
[j] Formicide cost = US$ 2.08 per 500 g (4 kg ha^{-}1).

certainly lead to higher plant density and lower costs per surviving plant.

Whereas in planting nursery-raised seedlings, seedling purchase represents the main factor that increases final costs, in our study that factor was weed control using manual herbicide application. Because of the small spacing between seeding locations (small enough to ensure high seedling densities), mechanical methods for weed control are not feasible; furthermore, other manual methods (using machetes or weed-whackers) are also not applicable, because of their low performance, high cost and the high probability of damaging the seedlings (Durigan et al., 2013). Moreover, the use of a non-selective, post-emergence, glyphosate-based herbicide led to the need to protect the seedlings with polyethylene covers, which also increased the operation time and costs. This was due to the lack of information and research data regarding the use of selective herbicides in restoration projects. A solution to this could be developing post-emergence herbicides not harmful to tree species or pre-emergence herbicides that reduce or eliminate only weed seed banks (Souza and Engel, 2017). Furthermore, to reduce environmental impacts of herbicide applications, an alternative might be using cover crops able to modify local microclimate and prevent weed development (Balandier et al., 2009).

4.6. Technical feasibility

Although the final costs were lower than those reported for planting nursery-raised seedlings, the final density of surviving seedlings two years after the first sowing (1265 ind.ha^{-1}) was also much lower than that expected for planting nursery-raised seedlings in similar tropical conditions (Rodrigues et al., 2009a). If we had conducted only one sowing, the results would be even more unsatisfactory.

The optimum density for forest restoration plantings depends on the urgency of establishing the plantation and the ground cover speed required, plus site conditions and the level of management to be carried out (Burton et al., 2006). A primary goal of a direct seeding system would be to achieve high ground cover quickly that would be effective in suppressing exotic, invasive grasses and allowing the arrival and establishment of new individuals. This goal was not achieved, partly due to poor species performance in this system, leading to the need for increased weeding operation frequency and duration to promote better seedling survival. This is also expected to increase the medium and long-terms costs.

Many authors report high final population density in their direct seeding experiments; however, they used a much higher seed density to achieve these results, namely 299,600 seeds.ha^{-1} (Araki, 2005) and 340,000–1,480,000 seeds.ha^{-1} (Isernhagen, 2010). These levels may be technically applicable, but would also increase seed purchase costs. Furthermore, the impact of removing seeds from natural ecosystems in large quantities over extended periods is still to be assessed as a possible constraint in the restoration of large areas by direct seeding (Durigan et al., 2013).

The most successful direct seeding plantings resulted from few species being sown (e.g. Dodd and Power, 2007; Engel and Parrotta, 2001; Knight et al., 1998). This method is valid for revegetation purposes only, and requires seed dispersal from neighboring sites (Engel and Parrotta, 2001) or the germination of native plants on the site (Cabin et al., 2002) to increase plant diversity. There is not currently enough evidence that these low biodiversity plantations are effective in achieving restoration goals in the long term. A tendency for stand simplification with age has been reported for older direct seeding plantations (Schneemann and McElhinny, 2012). Therefore, it is necessary to improve direct seeding techniques that use a higher richness of species sown, by surveying more species adapted to this system.

Other limitations for recommending direct seeding systems used on larger scales include the low seed availability in local markets, both in quantity and quality required (Douglas et al., 2007). Furthermore, most tropical forest species have recalcitrant seeds, which have low seed longevity and lose viability quickly when stored (Fonseca and Freire, 2003; Kaiser et al., 2014). As a consequence, commercial nurseries prefer to sell seedlings instead of seeds. Seed quality is vital to ensure germination in the field, since seeds with low vigor are unable to germinate in adverse conditions, and even when they do germinate, in most cases they do not generate vigorous seedlings (Botelho and Davide, 2002), hence decreasing direct seeding applicability on a large scale.

Considering the high dependence of seed germination and seedling survival on water, direct seeding plantings are more constrained to the rainy season than seedling plantings (Cabin et al., 2002; Dodd and Power, 2007; Douglas et al., 2007; Knight et al., 1998). Therefore, planting nursery-raised seedlings may be a more attractive method when the revegetation of areas is required for a longer period of the year.

Our results do not support the premise that direct seeding with a diverse tree species mixture is a promising option to restore tropical moist forests as a stand-alone technique. Other authors have also suggested direct seeding as a complementary technique for seedling plantings (Camargo et al., 2002; Cole et al., 2011; Isernhagen, 2010). As the best-performing species were the late successional species, which have large seeds, one possible alternative would be the planting of pioneer species by seedlings prior to sowing, with a later enrichment using late successional species by direct seeding. This would possibly be a more cost-effective option, considering that later successional species seedlings tend to be more expensive than the early successional ones in the local commercial nurseries. Furthermore, pioneer species seedlings would ensure fast ground cover and early suppression of grasses, decreasing maintenance costs.

5. Conclusions

Our results show that direct seeding of a mixture of forest species can have positive tradeoffs regarding forest restoration project costs; however, this technique has been proven to have several limitations. Based on our results, despite direct seeding is more cost-effective than planting nursery-raised seedlings; it is not possible to achieve high seedling density and high species diversity at short term, due to the great variability in species performances. Therefore, we need to better understand which species are suited to direct seeding systems, as well as to identify the main factors that affect germination, establishment and growth.

The results of our study indicate that the most suited species for direct seeding projects are non-pioneers with large seeds. Among our tested species, the most promising to direct seeding techniques are *E. pyriformis*, *H. courbaril*, *P. elegans*, *E. uniflora*, *I. vera* and *B. forficata*. Once most species had poor performance, it will be necessary to select more vigorous seeds or increase the density of seeds sown, especially for the species with low germination and establishment rates (pioneers with small seeds), in order to achieve higher seedling density and species diversity with this technique.

Further studies are needed to identify the most appropriate sowing times and to create less stressful conditions to facilitate seed germination and early seedling establishment, and reduce ecological filters, such as weed competition and microclimatic conditions. We recommend that direct seeding should be a complementary technique to seedling plantations, rather than using it as a stand-alone technique. Since non-pioneer species had better performances, introducing pioneer species as seedlings may be an alternative to achieve a higher ground cover more quickly.

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