LAND DEGRADATION & DEVELOPMENT
Land Degrad. Develop. (2015)
Published online in Wiley Online Library (wileyonlinelibrary.com) **DOI**: 10.1002/ldr.2421

IS DIRECT SEEDING A BIOLOGICALLY VIABLE STRATEGY FOR RESTORING FOREST ECOSYSTEMS? EVIDENCES FROM A META-ANALYSIS

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Received: 4 February 2015; Revised: 5 August 2015; Accepted: 5 August 2015

ABSTRACT

Ecological restoration has become an important technique for mitigating the human impacts on natural vegetation. Planting seedlings is the most common approach to regain lost forest cover. However, these activities require a large economic investment. Direct seeding is considered a cheaper and easier alternative technique, in which tree seeds are introduced directly on the site rather than transplanting seedlings from nurseries. To evaluate the effectiveness of direct seeding, we conducted a comprehensive search of the literature using 'restoration', 'direct seeding' and 'sowing' as keywords, and we performed a meta-analysis using 30 papers and 89 species. We used two different measures of restoration success: seed germination probability and success probability (the chance that a seed germinates and survives until the end of the experiment). In general, restoration attempts using direct-seeding techniques were relatively unsuccessful. On average, seed germination and success probability were 0·239 and 0·114, respectively, and were not affected by climate, species successional group or the application of pre-germinative treatments. Germination and success probability increased with seed size, and the use of physical protections resulted in a nearly twofold increase in germination probability, but this effect faded by the end of the experiments. Because of the low rate of seedling success, we suggest the use of direct seeding as a complementary technique to reduce restoration costs, particularly for species with large seeds and known high germination rates, but our results do not support direct seeding as a substitute for seedling planting. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: forest restoration; seed protection; seed germination; seedling success; seed size

INTRODUCTION

Around 13 million hectares of forests was converted to other uses or lost because of natural causes each year between 2000 and 2010 (FRA, 2010). The driving forces of land use vary in time and space according to specific human–environment conditions. Human alteration of landscapes from natural vegetation to other uses typically results in habitat loss, fragmentation and the loss of soil functions and services (Bierregaard *et al*., 2001; Keesstra *et al*., 2012; Brevik *et al*., 2015). However, natural regeneration of late-successional trees in fragmented and degraded landscapes can be strongly limited (Holl, 1999; Benítez-Malvido *et al*., 2001; Ceccon *et al*., 2003, 2004; Leitão *et al*., 2010). The lack of natural recruitment of these species has led to concerns about their persistence in fragmented and degraded landscapes, and aggressive restoration efforts have been suggested as a necessary step to augment severely dispersal-limited species in future forests (Martínez-Garza & Howe, 2003; Dosch *et al*., 2007). Moreover, forest recovery is the key to reduce soil losses and increase the quality of water and biodiversity (Keesstra, 2007; De la Paix *et al*., 2013), and there has been a huge effort performed to restore soils and ecosystems to avoid high erosion rates, pollution and soil degradation (Mekuria & Aynekulu, 2013; Novara *et al*., 2013; Paz-Ferreiro *et al*., 2014; Mekonnen *et al*., 2014, 2015).

In this context, ecological restoration has become an important restoration technique to mitigate the negative impacts of human activity on forest ecosystems (Chazdon, 2008; Benayas *et al*., 2009; Ceccon, 2013). The most common approach for generating vegetative cover in degraded sites is seedling planting. The simultaneous planting of pioneer and later-successional seedling species may accelerate the natural process of plant succession (Kageyama *et al*., 2003; Rodrigues *et al*., 2009). However, these activities are considered the most expensive in economic terms (Florentine *et al*., 2013). Thus, a major challenge for restoration programmes is to fulfil simultaneously both ecological and economic goals, and an important aspect of planning is the choice of an efficient planting technique (Campbell, 2002).

Direct seeding, in which tree seeds are introduced directly on the regeneration site, is considered a cheaper and easier alternative to transplanting seedlings previously produced in nurseries. Although rarely compared directly with seedling planting, the technique has been practised in North America (Moulton & Hernández, 2000) and Europe (Nabos & Epaillard, 1995), and recently in the tropics (Engel & Parrotta, 2001; Bonilla-Moheno & Holl, 2010).

The main advantages of direct seeding are the ability to sow large areas rapidly by hand or with broadcasting machinery and

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lower cost (around 50% according to Het, 1983) compared with transplanting seedlings (Engel & Parrotta, 2001; Camargo *et al.*, 2002). Additionally, field-grown plants are often less prone to toppling and have unhindered taproot formation compared with container-grown seedlings, which may develop restricted, 'cork-screw' roots and distorted taproots (Wennstrom *et al.*, 1999).

However, direct seeding also has a number of potential disadvantages, including difficulties in sourcing large quantities of viable seed, lack of information on optimum sowing times for many species, variability in starting and duration of germination, less flexibility to control conditions for seed germination and early seedling growth, predation of seed and seedlings and the need to control the intense competition from existing vegetation, particularly grasses. It is imperative that seeds of selected native species be available in sufficient quantities to meet requirements and be at a reasonable cost (Hooper *et al.*, 2005; Sampaio *et al.*, 2007). In fact, Derr & Mann (1971) recommended that when the viability of seeds is lower than 85%, it is best to use these seeds for sowing in nurseries, where conditions can be controlled to optimize germination, rather than directly sowing an excessive number of seeds. Derr & Mann (1971) also considered that the seedlings after direct seeding, in the first 2 years after germination, require more care, cleaning work and supervision than seedlings planted from nurseries.

Merritt & Dixon (2011) made a review and found the most common explanation for direct-seeding failure: a lack of research data on the phenology of seed development and maturation for most indigenous species that can lead to inappropriate timing of seed collection, a low quality and viability of collected seeds and poor storage procedures and inability to break seed dormancy that reduce the germination at the time seeds are sown. Florentine *et al.* (2013) also found that direct-seeding success depends on the variations in environmental conditions between years required for germination and seed survival.

Some other aspects of species or management may influence seed germination or seedling success at the restoration site, which in turn could influence the efficiency of direct-seeding techniques. Examples may include seed size, species successional group, climate of species occurrence, previous perturbation of habitat and the use of seed protectors.

The objective of this study is to review the effectiveness of the direct-seeding technique in forest restoration practices in terms of both the seed germination and success probabilities in various ecosystems using a meta-analysis. For each species found in our literature search, we scored ecological characteristics, including climate of species occurrence (tropical or non-tropical species), seed size (small, medium and large) and successional group (pioneer or non-pioneer). We also noted whether pre-germinative treatments or physical protectors were used in each field experiment. We hypothesized that while some species characteristics or techniques can improve the seed germination and success using direct seeding, this technique is viable for only a reduced number of species.

MATERIALS AND METHODS

We conducted an extensive survey of the literature published before April 2012 and after 1950 through computer searches on the databases available from Google Scholar and Web of Science at the Campus of the Universidade Federal do Parana, Brazil. Our queries included 'direct seeding' or 'direct sowing' and restoration as keywords (we also included the translated keywords in Portuguese and Spanish and wildcards of restoration such as restor*), as shown in Table I.

We found that Google Scholar gave more comprehensive results than did Web of Science. In fact, all relevant results from the Web of Science core collection were found in the search at Google Scholar, so this gave us confidence that our findings were representative and non-biased with the extra advantage that Google Scholar includes studies in

Table I. Query terms and databases

Database	Query sentence	Keywords included in results	Hits
Google Scholar[a]	'Direct seeding' and restoration	Direct seeding, seeding, restore, restoration, restoring	4,030
	'Direct sowing' and restoration	Direct sowing, sowing, restoring, restore	927
	'Semeadura direta' and restauração	Semeadura direta, restauração, restaurar	399
	'Siembra directa' and restauración	Siembra directa, restauración, restaurar	483
Web of Science[b]	TS = (direct seeding and restor[c]) And language: (English)	Direct seeding, seeding, restore, restoration, restoring	257
	TS = (direct sowing and restor[c]) And language: (English)	Direct sowing, sowing, restoring, restore	50
	TS = (semeadura direta and restaura[c]) And language: (Portuguese)	No results[d]	No results
	TS = (siembra directa and restaura[c]) And language: (Spanish)	No results[d]	No results

[a]Time range: 1950–2012 (April). Citations and patents not included. Queries performed automatically on title, abstract and body text fields. No wildcards used because Google Scholar automatically included variations of the term restoration, such as restored, restore and restoring.
[b]Time range: 1950–2012 (April). Queries on topic field. Type of document: all document types.
[c]Wildcard.
[d]Web of Science core collection of scientific documents does not include Portuguese or Spanish.

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Spanish and Portuguese and other documents such as post-graduate thesis and technical reports. A total of 5,890 references were retrieved from all four query sentences used in Google Scholar and 307 from the Web of Science (Table I). Google Scholar allows only 1,000 references to be examined at any one query. To overcome this limitation, we divided the search in several time periods as to have less than 1,000 results in each. For example, for the query 'direct seeding' and restoration, on the 1951–1970 range, there were 33 results. However, for the range 2008–2010, there were 981 results. In this way, we were able to review all results for all the query sentences used. Our oldest identified relevant study has a date of 1967, and our most recent was of 2012. From that total, we eliminated redundancies systematically and also selected only those dealing with forest terrestrial ecosystems (studies dealing with shrubs, grasslands, mangroves, etc. were not considered).

A further criterion was to ignore studies on reforestation, which is very common in temperate ecosystems, because we focus on restorations approaches only. A very small number of papers were not considered because the full-text option was not available, and the authors did not respond to our request for reprints. The resulting publications were subsequently reviewed to determine whether they met the criteria previously established and required by the meta-analysis, the study has to report, as a result from a field work, the probability of seed germination, seedling survival or both (to obtain success probability, which means the chance that a seed germinates and survives until the end of the experiment), resulting in 125 selected studies. However, for the meta-analysis, it was also necessary that these studies report the 'exact' number of sown seeds. This last condition yields a total of 30 studies as reported in Appendix 1 and Appendix 2. Many studies on temperate ecosystems presented only the amount of sowed seeds in weight rather than in number (mostly because these species have very small seeds); for consistency, we chose not to include these studies. The 30 studies included a total of 89 species examined.

We systematically extracted experiment information from the text, tables and figures of the selected papers. To obtain accurate information from figures, we used DATATHIEF (v1.6), a shareware program that extracts data points from graphs (www.datathief.org). We also contacted authors for complementary information, although this allowed the inclusion of only one additional study in our analysis.

The research works included both single-species and multi-species studies, and experiments varied in their use of pre-germinative treatments (seed scarification) and physical protection of sown seeds (using wood veneer or bottomless plastic cup). We considered each species and experiment as one case in the meta-analysis, resulting in 89 species and 30 direct-seeding restoration studies. Seedling survival was evaluated in only 60 species in five studies.

Variables used in the meta-analysis such as 'climate' was obtained from the methodology (study site) of the papers; however, there was parsimony in the classification to facilitate the meta-analysis. For example, 'tropical' climate could be humid, seasonal dry and so on. Many papers showed the seed size and the successional group of used species; otherwise, we searched in the literature.

We used two different measures of restoration success: germination probability and success probability. The latter was calculated as the fraction of sown seeds that germinated and survived to the end of the experiment (i.e. germination probability × survival probability).

To perform a meta-analysis we required the following: (1) effect sizes; (2) the weights associated with them; and (3) a statistical test. An effect size is the result of an experiment measured in a way that is comparable across studies. Using the numbers of sown seeds, number of seedlings germinated and number of survivors to the end of the experiment (if measured), we estimated the germination and success probabilities. Both measurements were arcsine transformed to attain normality and used as effect sizes. Larger sample sizes lend more support to experimental results and thus are given more weight in meta-analyses. The effect sizes and weights were estimated using the METAFOR package (Viechtbauer, 2010) in R (R Core Team, 2012).

To determine which variables (application of pre-germinative treatments, physical protection, climate, seed size and successional group) had an effect on germination or success probabilities, we used generalized linear mixed-effects models as the statistical test of the meta-analysis with the MCMCglmm package (Hadfield, 2010) in R. The response variable was assumed to be normally distributed, and an identity link was specified. Effect size weights were included in the analyses.

Most studies reported data for more than one species, which were subject to the same experimental protocol, study site and climate conditions occurring during the experiment. As a result, germination and success probabilities of all species in a given study may not be independent. To account for this, we specified study as a random factor. Climate, seed size, successional group, pre-germinative treatment and physical protection were considered as fixed factors. A separate analysis was conducted for each of these variables, as sample sizes for estimating interactions were usually too small and statistical power too low to include more than one variable at a time. We compared the posterior distributions obtained through Markov chain Monte Carlo sampling using a non-informative prior (Hadfield, 2010).

RESULTS

Studies were carried out in 13 different countries. Brazil presented the largest number of studies (around 32·5%) followed by Australia (12·5%, Appendix 1). Most of the cases were in tropical areas (71·8%), 11·8% in temperate, 10·6% in subtropical and 5·8% in tropical altitude (Appendix 1). Most of the direct-seeding restoration experiments were carried out in pastures (40·74%), mining areas (14·38%) and secondary forests (8·93%, Figure 1).

On average, germination and success probabilities were quite small (0·239 and 0·114, respectively). Germination

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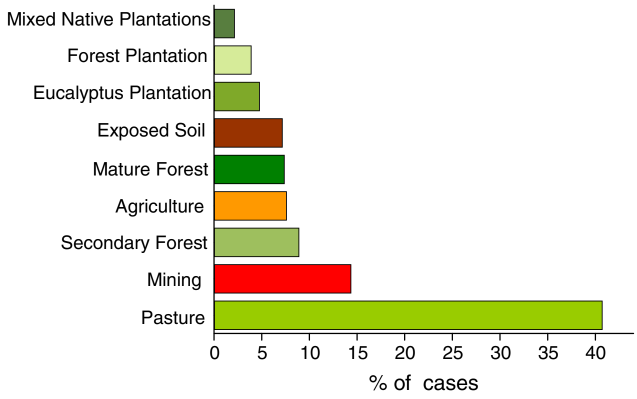

Figure 1. Percentage of the types of disturbed habitat prior to restoration. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

and success probabilities were also low (<0·2) in a large percentage of species (47% for germination and 72% for success). However, although relatively rare, some species did present a high probability (>0·41) of germination and success (14·6% and 10%, respectively; Annex 1, Figure 2). These figures were virtually unchanged by different climates, application of pregerminative treatments or successional group, suggesting that the lack of statistical differences was due to a weak effect of these explanatory variables, rather than to insufficient statistical power.

Seed size did have a significant effect on germination and success. Large seeds had a germination probability twice as large as that of small ones, while germination of intermediate-sized seeds was indistinguishable from the other two groups (Figure 3). The same pattern was observed for success probability, with an even larger difference between large and small seeds (Figure 3).

The use of physical protection of seeds resulted in a nearly twofold increase of germination probability, but this effect faded by the end of the experiments, as no difference in success probability between protected and unprotected plots was found (Figure 4).

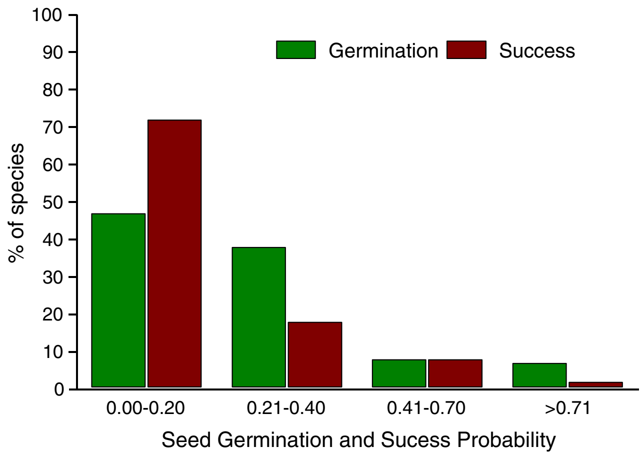

Figure 2. Distribution of germination and success probability ranks among species. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

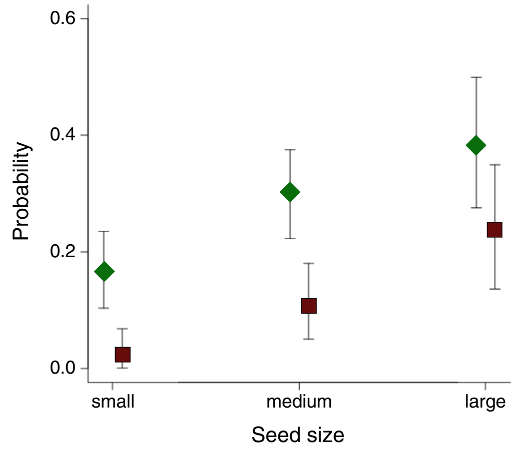

Figure 3. Mean germination (green diamonds) and success (brown squares) probabilities for different seed sizes. Bars represent the 95% confidence intervals of the posterior distributions. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

DISCUSSION

There was a high variability of previous perturbation events in restored habitats among the studies evaluated; however, abandoned pastures were the most commonly used for direct-seeding restoration (41%); this is because pasture establishment is a primary cause of deforestation in tropical landscapes (Ospina *et al*., 2012). In the present study, most of the reviewed cases of direct seeding were carried out in tropical areas (71·8%) that are the largest affected ecosystems in the world by land use change (Aide *et al*., 2012). In these, pasture has been regarded as an important cause of deforestation in the last decades (Fearnside, 1993).

In general, restoration attempts using the direct-seeding technique were relatively unsuccessful in terms of seed germination and success probabilities. Most of the species (72%) presented a low success probability (<0·20), highlighting the risk of relying solely on direct-sown seeds in a restoration project. In fact, Kettle *et al*. (2011) suggested that only seeds that can tolerate drying and long-term storage could be established, because the data that exist on seed behaviour in four of the globally most

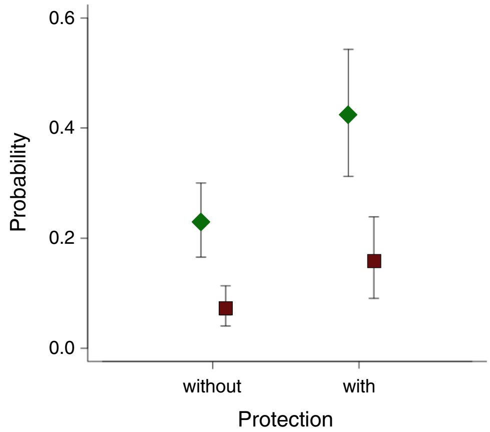

Figure 4. Mean germination (green diamonds) and success (brown squares) probabilities for experiments based on use of seed protection. Bars represent the 95% confidence intervals of the posterior distributions. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

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important timber families indicate that, on average, 60% cannot (Kew Royal Botanic Gardens, n.d.). In this study, the highest germination probability was exhibited by two non-pioneer species from the tropics, *Garcinia intermedia* ($p = 0{\cdot}90$) and *Enterolobium contortisiliquum* ($p = 0{\cdot}86$; Appendix 1). However, the average seedling success probability of the latter was very low ($p = 0{\cdot}01$). In fact, in the natural regeneration of many types of forests, seed germination is high, and seedling survival is frequently low (Ceccon *et al*., 2003, 2004; Pérez-Ramos & Marañón, 2012). Two other species that could be highly recommended for direct-seeding restoration are the pioneer *Erythrina velutina* and the non-pioneer *Hymenaea courbaril* also from the tropics, owing to their high germination and moderate seedling success probability. Even though the tropical pioneer species *Senna multijuga* showed a not so high germination ($p = 0{\cdot}40$) and a high seedling success ($p = 0{\cdot}86$), it could also be recommend (Appendix 1).

It is also important to consider that low germination and success rates in direct-seeding restoration may imply considerable loss of the initial investment such as seed collection, seed cleaning, pre-germinative treatment, land preparation and sown seeds in the field. These initial expenditures are also present in the restoration by seedlings; however, a few comparative studies have shown a considerably higher survival in restoration using planting seedlings rather than direct seeding. In a tropical zone, Ray & Brown (1995) compared three strategies of restoration using the same group of species: direct seeding, planting seedlings and planting rooted cuttings in a dry forest plant community at St John, US Virgin Islands. In this case, restoration from planting seedlings survived best (52%) over an initial 9-month period. Cuttings of six species rooted successfully in a shade house, but only two of these species survived the 9-month field experiment. Seed germination in direct seeding was low, under 11%, for 8 of the 10 species tested, and 4 species did not germinate at all. In temperate areas in Denmark and Sweden, Madsen & Löf (2005) evaluated the establishment of *Quercus robur* using direct seeding and planting seedlings. The mean establishment percentages in direct seeding varied around between 20% and 50% while in planting seedlings they varied between 50% and 100%.

On the other hand, in direct seeding, seed size influenced seed regeneration and seedling success. Large seeds presented the highest germination and success probabilities. Larger-seed species generally have the advantage that they can germinate at a broader range of temperatures than smaller-seed species (Burton & Bazzaz, 1991). Large seeds also have large nutrient reserves and energy stock and therefore have the ability to rapidly develop a long taproot. This in turn presumably allows them to survive short periods of drought or other stresses (Tripathi & Khan, 1990; Beckage & Clark, 2003; Willoughby *et al*., 2004). Cerdà & Garcıa-Fayos (2002) and Wang *et al*. (2012) also found that small-seed species suffered the highest rates of washing away when compared with large-seed species. Furthermore, large seeds confer seedlings with a competitive advantage (Turnbull *et al*., 1999, 2004) particularly in systems that have become covered by grasses (41% of direct-seeding cases, Figure 1).

The use of physical protection of seeds (wood veneer or bottomless plastic cup) increased germination by nearly twofold, because they create a microenvironment for the germination of seeds and reduce the occurrence of burial or washing away of seeds when soil is moved by rainwater (Mattei 1997; Cerdà & Garcıa-Fayos, 2002; Wang *et al*., 2012). However, sometimes seed transport by overland flow may lead to seed redistribution. According to the Bochet (2015) literature review, the directed short-distance displacement of seeds to suitable sites, where they are preferentially trapped by the vegetated patches, may result in maintaining the patchiness dynamic of the system. On the other hand, seed protection helps avoid seed predation mainly by ants and birds (Ferreira *et al*., 2009). Seed predation may have an especially strong impact on seedling recruitment. Indeed, in stable populations of four species of long-lived perennials in sclerophyllous vegetation of south-eastern Australia, seed predators were estimated to destroy an average of 95% of seeds (Andersen, 1989).

Mainly because of the low seedling success for most species, if in a large-scale restoration project, there is no alternative to direct seeding, it is strongly recommended, before the field establishment, to conduct scientific experiments with several species to identify those that have a high percentage of germination and survival in the field. However, any previous research may impact the costs of direct seeding and would possibly result in the successful restoration of only a low number of species.

Direct seeding may be recommended as a complementary restoration technique mainly in agricultural landscapes when a large diversity of species is needed in the restoration project. An emblematic example is the case of well-known experience in Brazil (Rodrigues *et al*., 2009). The Laboratory of Ecological Restoration (LER) of the University of São Paulo, in Brazil, after nearly 30 years of experience in restoring the Brazilian Atlantic Forest, seems to have found a very successful method for the predominant agriculture landscape of the region (Brancalion *et al*., 2009). This research group found that at least 80 species are needed in a successful restoration project in the region. A project involving such a large number of species turns easily into an expensive enterprise, and because of this, a portion of the restoration is made with planting seedlings, and the diversity of species is increased using direct seeding. The LER is constantly researching on the most successfully species in direct seeding (Fakin, 2005; Isernhagen, 2010).

CONCLUSIONS

Because of the low germination and seedling establishment success, direct seeding should not be recommended as the sole restoration technique. Most of the species (72%) presented a low success probability ($<0{\cdot}20$); therefore, the selection of species in the direct-seeding projects must be carried out carefully to have a favourable cost : benefit ratio. This species selection should start with those with high seed

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viability and large size. The use of physical protections may increase germination probability in direct seeding, although overall success may not be affected. Because of the low rate of recruitment, we suggest the use of direct seeding as a complementary technique of planting seedlings to improve species diversity, when seed viability and size of the species used are previously known.

ACKNOWLEDGEMENTS

Eliane Ceccon very much appreciates PAPIIT-UNAM grants IN300615 and IN105015. Authors also thank J. M. Torezan and M. Suganuma for giving us their raw data and Marcia Marques and Natacha Sobanski for their help in most of the phases of the study. We also thank Lynna Kiere and Octavio Miramontes for useful comments.

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APPENDIX 1

Germination probability (G) and success probability (S) of species and families including climate and functional group (FG)

References	Country	Species	Family	Climate	FG	G	S
Cole *et al*., 2011	Costa Rica	*Garcinia intermedia*	Clusiaceae	Tropical altitude	Non-pioneer	0·90	0·65
Klein, 2005 Aragão, 2009 Ferreira *et al*., 2009 Engel & Parrota, 2001	Brazil Brazil Brazil Brazil Brazil	*Enterolobium contortisiliquum*	Fabaceae	Subtropical	Non-pioneer	0·86	0·01
Laliberté *et al*., 2008	Canada	*Quercus rubra*	Fagaceae	Temperate	Pioneer	0·82	
Klein, 1999	Brazil	*Peltophorum dubium*	Fabaceae	Subtropical	Pioneer	0·81	
Santos, 2010a	Brazil	*Erythrina velutina*	Fabaceae	Tropical	Pioneer	0·80	0·57
Ferreira *et al*., 2009 Aragao, 2009	Brazil Brazil	*Hymenaea courbaril*	Fabaceae	Tropical	Non-pioneer	0·72	0·67
Santos, 2010a	Brazil	*Sapindus saponaria*	Sapindaceae	Tropical	Non-pioneer	0·57	0·44
Barbosa, 2008 Carrijo *et al*., 2009	Brazil	*Eriotheca pubescens*	Malvaceae	Tropical	Pioneer	0·58	0·25
Ferreira *et al*., 2009 Aragao, 2009	Brazil	*Cassia grandis*	Fabaceae	Tropical	Pioneer	0·56	0·52
Wang *et al*., 2011	China	*Castanopsis chinensis*	Fagaceae	Subtropical	Pioneer	0·54	0·21
Sunganuma *et al*., 2008	Brazil	*Diospyros brasiliensis*	Ebenaceae	Tropical	Non-pioneer	0·46	
Laliberté *et al*., 2008	Canada	*Quercus macrocarpa*	Fagaceae	Temperate	Pioneer	0·45	
Camargo *et al*., 2002	Brazil	*Caryocar villosum*	Caryocaraceae	Tropical	Non-pioneer	0·42	0·21
Ferreira *et al*., 2007	Brazil	*Senna multijuga*	Caesalpiniaceae	Tropical	Pioneer	0·40	0·87
Camargo *et al*., 2002	Brazil	*Simarouba amara*	Simaroubaceae	Tropical	Non-pioneer	0·40	0·34
Hooper *et al*., 2002	Panamá	*Ormosia macrocalyx*	Fabaceae	Tropical	Non-pioneer	0·40	0·30
Hooper *et al*., 2002	*Panamá*	*Genipa americana*	Rubiaceae	Tropical	Non-pioneer	0·40	0·25
Camargo *et al*., 2002.	Brazil	*Calophyllum longifolium*	Clusiaceae	Tropical	Non-pioneer	0·40	0·24

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APPENDIX 1 (CONTINUED)

References	Country	Species	Family	Climate	FG	G	S
Wang *et al*., 2009	China	*Cryptocarya chinensis*	Lauraceae	Subtropical	Non-pioneer	0·39	0·09
Santos, 2010a	Brazil	*Bowdichia virgilioides*	Fabaceae	Tropical	Pioneer	0·39	0·04
Cole *et al*., 2012	Costa Rica	*Ruagea glabra*	Meliaceae	Tropical altitude	Non-pioneer	0·38	0·06
Hooper *et al*., 2002	Panamá	*Dipteryx panamensis*	Fabaceae	Tropical	Non-pioneer	0·37	0·29
Jinks *et al*., 2006	England	*Fraxinus excelsior*	Oleaceae	Temperate	Pioneer	0·37	
Santos, 2010a	Brazil	*Lonchocarpus sericeus*	Fabaceae	Tropical	Non-pioneer	0·36	0·30
Erefur *et al*., 2008	Norway	*Picea abies*	Pinaceae	Temperate	Non-pioneer	0·35	
Aragao, 2009 Ferreira *et al*., 2009	Brazil Brazil	*Schinus terebinthifolius*	Anacardiaceae	Tropical	Pioneer	0·35	0·20
Florentine *et al*., 2013	Australia	*Acacia retinodes*	Fabaceae	Temperate	Pioneer	0·34	
Doust *et al*., 2008	Australia	*Castanospermum australe*	Fabaceae	Tropical	Non-pioneer	0·34	
Florentine *et al*., 2013	Australia	*Eucalyptus viminalis*	Myrtaceae	Temperate	Pioneer	0·33	
Cole *et al*., 2010	Costa Rica	*Otoba novogranatensis*	Myristicaceae	Tropical altitude	Non-pioneer	0·31	0·05
Jinks *et al*., 2006	*England*	*Acer pseudoplatanus*	Aceraceae	Temperate	Pioneer	0·30	
Camargo *et al*., 2002.	Brazil	*Cariniana micrantha*	Lecythidaceae	Tropical	Non-pioneer	0·29	0·06
Cole *et al*., 2012	Costa Rica	*Pseudolmedia spuria*	Moraceae	Tropical altitude	Pioneer	0·29	0·05
Camargo *et al*., 2002.	Brazil	*Buchenavia grandis*	Combretaceae	Tropical	Non-pioneer	0·29	0·00
Hooper *et al*., 2002	Panamá	*Carapa guianensis*	Meliaceae	Tropical	Pioneer	0·28	0·23
Santos, 2010a	Brazil	*Guazuma ulmifolia*	Sterculiaceae	Tropical	Pioneer	0·28	0·15
Carvalheira, 2007 Santos, 2010b	Brazil Brazil	*Enterolobium gummiferum*	Fabaceae	Tropical	Non-pioneer	0·27	0·08
MoheNot & Holl, 2010	Brazil	*Enterolobium cyclocarpum*	Fabaceae	Tropical	Non-pioneer	0·27	0·05
Wang *et al*., 2011	China	*Psychotria rubra*	Rubiaceae	Subtropical	Non-pioneer	0·27	0·03
Cole *et al*., 2011	Costa Rica	*Calophyllum brasiliense*	Clusiaceae	Tropical altitude	Non-pioneer	0·26	0·03
Eis, 1967		*Picea glauca*	Pinaceae	Temperate	Pioneer	0·24	0·15
Sunganuma *et al*., 2008	Brazil	*Achatocarpus pubescens*	Achatocarpaceae	Tropical	Non-pioneer	0·24	
Engel & Parrota, 2001	Brazil	*Schizolobium parahyba*	Fabaceae	Tropical	Pioneer	0·24	
Hooper *et al*., 2002	Panamá	*Virola surinamensis*	Myristicaceae	Tropical	Non-pioneer	0·23	0·16
Doust *et al*., 2008	Australia	*Acacia celsa*	Fabaceae	Tropical	Pioneer	0·23	0·00
Erefur *et al*., 2008 Nilson & Hjältén, 2003 Wennström *et al*., 1998	Norway Sweden Sweden	*Pinus sylvestris*	Pinaceae	Temperate	Pioneer	0·22	0·14
Ferreira *et al*., 2007	Brazil	*Solanum granuloso-leprosum*	Solanaceae	Tropical	Pioneer	0·21	0·09
Aragão, 2009 Ferreira *et al*., 2009	Brazil	*Caesalpinia leyostachya*	Fabaceae	Tropical	Pioneer	0·20	0·15
Santos, 2010a Carvalheira, 2010	Brazil Brazil	*Hymenaea stigonocarpa*	Fabaceae	Tropical	Non-pioneer	0·19	0·05
Camargo *et al*., 2002	Brazil	*Parkia multijuga*	Mimosoideae	Tropical	Non-pioneer	0·18	0·04
Camargo *et al*., 2002	Brazil	*Dinizia excelsa*	Mimosoideae	Tropical	Non-pioneer	0·18	0·03
Sunganuma *et al*., 2008	Brazil	*Cordia ecalyculata*	Boraginaceae	Tropical	Pioneer	0·18	
Florentine *et al*., 2013	Australia	*Eucalyptus camaldulensis*	Myrtaceae	Temperate	Pioneer	0·18	
Camargo *et al*., 2002	Brazil	*Parkia pendula*	Mimosoideae	Tropical	Non-pioneer	0·17	0·01
Santos, 2010a	Brazil	*B. virgilioides*	Fabaceae	Tropical	Pioneer	0·16	0·00
MoheNot & Holl, 2010	Mexico	*Manilkara zapota*	Sapotaceae	Tropical	Non-pioneer	0·15	0·03
Jurado *et al*., 2006	Mexico	*Leucaena leucocephala*	Fabaceae	Tropical	Non-pioneer	0·14	
Aerts *et al*., 2006	Ethiopia	*Olea europaea* ssp. *cuspidata*	Oleaceae	Tropical	Non-pioneer	0·14	
Jurado *et al*., 2006	Mexico	*Prosopis laevigata*	Fabaceae	Tropical	Non-pioneer	0·14	
Sun *et al*., 1995 Doust, 2008	Australia Australia	*Alphitonia petriei*	Rhamnaceae	Tropical	Pioneer	0·10	0·27
	Brazil	*Euterpe edulis*	Arecaceae	Tropical	Non-pioneer	0·12	

(*Continues*)

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APPENDIX 1 (CONTINUED)

References	Country	Species	Family	Climate	FG	G	S
Sunganuma *et al*., 2008							
Hooper *et al*., 2002	Panamá	*Byrsonima crassifolia*	Malpighiaceae	Tropical	Pioneer	0·10	0·03
Santos-Junior, 2004	Brazil	*Copaifera langsdorffii*	Fabaceae	Tropical	Non-pioneer	0·10	0·02
Santos, 2010b	Brazil						
Carvalheira, 2007	Brazil						
Jurado *et al*., 2006	Mexico	*Acacia berlandieri*	Fabaceae	Tropical	Pioneer	0·10	
Camargo *et al*., 2002	Brazil	*Triplaris surinamensis*	Polygonaceae	Tropical	Non-pioneer	0·09	0·00
Florentine *et al*., 2013	Australia	*Acacia pycnantha*	Fabaceae	Subtropical	Pioneer	0·08	0·08
Thrall *et al*., 2005	Australia						
Jurado *et al*., 2006	Mexico	*Ebenopsis ebano*	Fabaceae	Tropical	Pioneer	0·08	
Jurado *et al*., 2006	Mexico	*Havardia pallens*	Fabaceae	Tropical	Pioneer	0·08	
Engel & Parrota, 2001	Brazil	*Ceiba speciosa*	Malvaceae	Tropical	Pioneer	0·08	
Doust *et al*., 2008	Australia	*Cryptocarya oblata*	Lauraceae	Tropical	Non-pioneer	0·08	
Camargo *et al*., 2002		*Jacaranda copaia*	Bignoniaceae	Tropical	Pioneer	0·07	0·00
Hooper *et al*., 2002	Panamá	*Annona spraguei*	Annonaceae	Tropical	Pioneer	0·07	0·04
Santos, 2010a	Brazil	*Machaerium aculeatum*	Fabaceae	Tropical	Pioneer	0·06	0·04
Hooper *et al*., 2002	Panamá	*Heisteria concinna*	Olacaceae	Tropical	Non-pioneer	0·06	0·00
Camargo *et al*., 2002	Brazil	*Cochlospermum orinoccense*	Cochlospermaceae	Tropical	Pioneer	0·05	0·00
Camargo *et al*., 2002	Brazil	*Ochroma pyramidale*	Bombacaceae	Tropical	Pioneer	0·05	0·00
Florentine *et al*, 2013	Australia	*Acacia dealbata/mearnsii*	Fabaceae	Subtropical	Pioneer	0·04	
Thrall *et al*., 2005	Australia						
Doust *et al*., 2008	Australia	*Flindersia brayleyana*	Rutaceae	Tropical	Non-pioneer	0·04	
Thrall *et al*., 2005	Australia	*Acacia paradoxa*	Fabaceae	Subtropical	Pioneer	0·03	0·08
Thrall *et al*., 2005	Australia	*Acacia acinacea*	Fabaceae	Subtropical	Pioneer	0·03	0·03
Suganuma *et al*., 2008	Brazil	*Annona cacans*	Annonaceae	Tropical	Pioneer	0·03	
Hooper *et al*., 2002	Panamá	*Hampea appendiculata*	Malvaceae	Tropical	Pioneer	0·02	0·00
Suganuma *et al*., 2008	Brazil	*Vitex montevidensis*	Verbenaceae	Tropical	Pioneer	0·02	
Engel & Parrota, 2001	Brazil	*Mimosa scabrella*	Fabaceae	Tropical	Pioneer	0·01	
Engel & Parrota, 2001	Brazil	*Croton floribundus*	Euphorbiaceae	Tropical	Pioneer	0·00	

APPENDIX 2

References of papers used in the meta-analysis

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