Research Article

Responses of transplanted native tree species to invasive alien grass removals in an abandoned cattle pasture in the Lacandon region, Mexico

Francisco J. Román-Dañobeytia[1,2]*, Jorge Castellanos-Albores[1], Samuel I. Levy-Tacher[1], James Aronson[3,4], Neptalí Ramírez-Marcial[1], Ricardo Ribeiro Rodrigues[5]

[1]*El Colegio de la Frontera Sur, ECOSUR, Carretera Panamericana y Periférico Sur s/n, C.P. 29290, San Cristóbal de Las Casas, Chiapas, México.*

[2]*Current Address: Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancón, Panamá.*

[3]*Centre d'Ecologie Fonctionnelle et Evolutive (CNRS-U.M.R. 5175), 1919, Route de Mende, 34293 Montpellier, France.*

[4]*Missouri Botanical Garden, 4344 Shaw Blvd., P.O. Box 299, St. Louis, MO 63166-0299, U.S.A.*

[5]*Laboratório de Ecologia e Restauração Florestal, LCB/ESALQ, Universidade de São Paulo, Avenida Pádua Dias 11, P.O. Box 9, CEP 13.418-900 Piracicaba, São Paulo, Brazil.*

*Correspondence author. E-mail: fromn76@gmail.com; telephone number: + 507 2128234.

Abstract

We tested the early performance of 16 native early-, mid-, and late-successional tree species in response to four intensities of grass removal in an abandoned cattle pasture dominated by the introduced, invasive African grass, *Cynodon plectostachyus*, within the Lacandon rainforest region, southeast Mexico. The increase in grass removals significantly improved the performance of many species, especially of early- and mid-successional species, while performance of late-successional species was relatively poor and did not differ significantly among treatments. Good site preparation and at least one additional grass removal four months after seedling transplant were found to be essential; additional grass removals led to improved significantly performance of saplings in most cases. In order to evaluate the potential of transplanting tree seedlings successfully in abandoned tropical pastures, we developed a "planting risk index", combining field performance measurements and plantation cost estimations. Our results showed a great potential for establishing restoration plantings with many early- and mid- successional species. Although planting risk of late-successional species was considered high, certain species showed some possibilities of acclimation after 18 months and should be considered in future plantation arrangements in view of their long-term contributions to biodiversity maintenance and also to human welfare through delivery of ecosystem services. Conducting a planting risk analysis can help avoid failure of restoration strategies involving simultaneous planting of early-, mid-, and late-successional tree species. This in turn will improve cost-effectiveness of initial interventions in large-scale, long-term restoration programs.

Key-words: Forest restoration, plantation costs, planting risk index, successional groups, tropical rainforest.

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Introduction

Restoration actions are increasingly being implemented throughout the world, supported by global policy commitments such as the Convention on Biological Diversity, the Kyoto Protocol, and the United Nations Framework Convention on Climate Change [1, 2]. 'Hard' legislation requiring mitigation, offsets, and even forest restoration linked to industrial, commercial, and urban activities is also gaining ground [3]. Nonetheless, restoring stable forest functions - in tropical forests, especially - requires high species diversity at the landscape scale [4, 5]. Particularly in light of global climatic change scenarios, which predict more frequent extreme disturbances and climatic events, it is important to incorporate insights from the relation between biodiversity and stability of ecosystem function into forest restoration projects [6, 7]. Rather than focusing on species per se, focusing on functional diversity of tree species assemblages seems appropriate when selecting tree species for restoration [8, 9].

Across the tropics, millions of hectares of forest have been converted to cattle pasture and then abandoned [6]. Invasive alien grass species such as *Cynodon plectostachyus*, and many others originally introduced as pasture plants, commonly form dense, monospecific stands in tropical pastures, resulting in the inhibition of natural or induced tree regeneration by competitive interactions and the occurrence of fires [10, 11]. As a consequence, vast areas of the tropics are now characterized by agricultural mosaics of pastures and fields interrupted by occasional forest remnants, a scenario that presents significant new challenges to conservation and restoration [12, 2].

One of the most successful, and attractive, restoration methods proposed to date for tropical forests is based on the idea of planting tree species from different functional groups representing the main successional stages of forest ecosystems [13, 14, 15]. In such methods, early-successional trees, which are typically fast-growing and wide canopy species, are planted together with slow-growing and narrow canopy mid- and late-successional species in plantings that cover the entire area targeted for restoration [16, 17, 18]. For example, in the Brazilian Atlantic Forest, researchers at the University of São Paulo have developed a succession-based model which consists of 'filling' and 'diversity' planting lines [19]. In the 'filling' line, 15–30 early-successional species are planted to promote fast soil coverage and improve environmental conditions near the ground. On the other hand, the 'diversity' line receives 70–80 mid- and late-successional tree species (and also pioneers with poor soil coverage) that, distributed in proper densities, will promote the long term development and self-maintenance of the forest structure, and introduce more functional diversity into the system.

As in forests everywhere, a key stage in tropical forest restoration is the performance of seedlings during the first year or two after trees are planted [20, 21]. Good site preparation will get seedlings off to a fast start, but in tropical regions especially, weed competition must be controlled until the trees are well established and canopy closure occurs [22, 23]. Previous studies of young plantations in tropical regions suggest that aggressive grass control treatments prevent the risk of fire and the physical smothering of trees, reduce weed maturation and seed production, and minimize rodent habitat [21, 24]. However, grass removals are costly and therefore must be evaluated in terms of cost-effectiveness.

This study explores the potential to reintroduce locally preferred native tree species that also cover a range of functional types, in order to accelerate the forest recovery process, and to provide a variety of forest goods and services that local people appreciate. We established a field experiment to test the effect of grass removals on the early performance of transplanted seedlings of 16 native early-, mid-, and late-successional tree species in our long-term study area in southeastern Mexico. Different intensities of grass removal were implemented and compared in order to identify the most cost-effective strategy to achieve satisfactory seedling establishment for each candidate species in *Cynodon plectostachyus* abandoned pastures. We hypothesized that seedling performance should increase with the number of grass removals. Concurrently, we expected that the number of repetitions required, and the overall cost of grass removals, would be less for fast-growing tree species than for slow-growing species.

Methods

Study area

The study was carried out at Nueva Palestina (lat 16°50'N, long 91°15W) located within the Lacandon Community, which covers an area of 2526.31 km^2 in the Lacandon region of Chiapas, southeast Mexico (Fig. 1). Nueva Palestina is situated in the northeastern portion of the Montes Azules Biosphere Reserve (3300 km^2), one of the largest and most important protected areas of evergreen tropical rainforest in Mexico and in all of Mesoamerica [25]. Landscapes in Nueva Palestina, and in the Lacandon Community as well, consist primarily of agricultural and pasture lands, secondary forests, and small patches of mature forest fragments [26].

Prevailing climate in this region is humid and warm (mean annual temperature of 24.7°C; mean temperature of 18°C during the coldest month of the year, January). Mean annual rainfall is c. 2,000 mm, with the majority falling between June and September. A short dry season, with less than 60 mm rainfall per month, occurs between February and April [27].

Predominant soil types are humic acrisols associated with rendzina and are located above calcareous substrates; they are clay-like and present high contents of soil organic matter in undisturbed forest [28]. Land tenure is mainly communal, and economic activities include cropping of maize, beans, and peppers (*Capsicum* spp.), with extensive cattle ranching being common as well [26].

The experimental site was used for cattle ranching for c. 30 years prior to being reallocated by the local community, in 1992, to the construction and establishment of a secondary school. Before our experiment began in 2007, the site was dominated by the rhizomatous *Cynodon plectostachyus* (K. Schum.) Pilg., a C_4 grass native to southern Africa. Known in horticulture as Star grass, this fast-growing species reaches 1.0–1.5 m in height, and quickly forms dense stands that inhibit regeneration of native trees due to the unfavorable microsite conditions for tree species recruitment, and intense competition once they germinate [29, 10]. These site characteristics are present in many abandoned pastures within the Lacandon region and elsewhere in the tropics, and thereby represent an opportunity to test the viability of an approach to restoration plantings that could provide important benefits to local communities and help improve the effectiveness of projects and programs aimed at restoring tropical forest ecosystems worldwide.

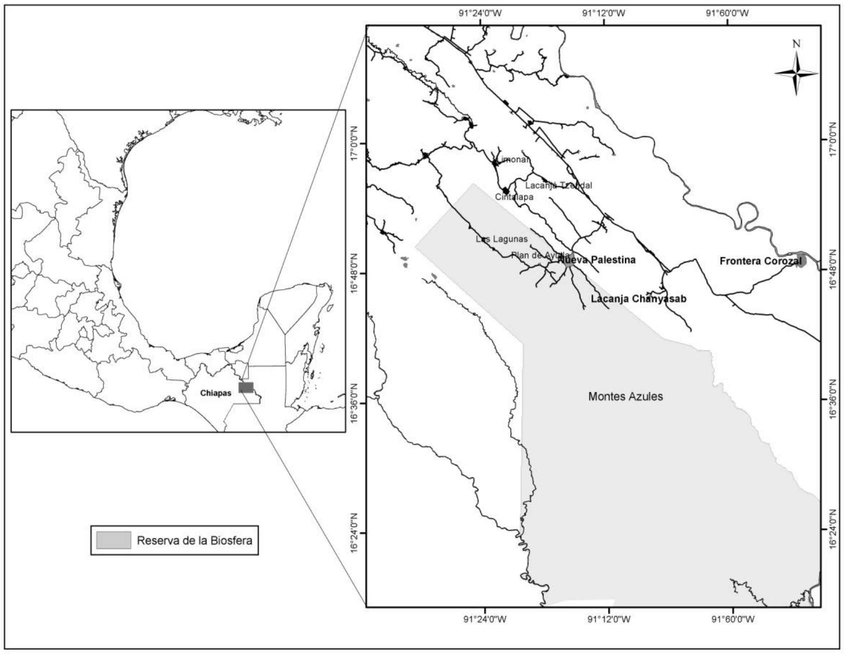

Fig. 1. Map of the Lacandon rainforest region showing the study area Nueva Palestina in the northeastern portion of the Montes Azules Biosphere Reserve.

Species selection

Sixteen native tree species widely distributed across tropical America were chosen to represent a range of ecological characteristics, as well as to assess the viability of planting mixtures of early-, mid-, and late-successional tree species simultaneously in abandoned cattle pastures. Additionally, species selection also took into account preferred native tree species of ethnobotanical interest, or with known commercial use (Appendix 1). Based on a secondary succession sequence documented previously in the study area [30] we grouped the 16 tree species into three successional groups. The first group, considered as "early-successional," included four typical pioneer species able to grow in open areas. The second group, considered as "mid-successional," included seven species which are also able to develop in open areas but generally live longer and grow taller than species from the first group. Finally, the third group of "late-successional" species included five typical shade-tolerant species that are present in mature forests and are highly appreciated for their hard and valuable wood (Appendix 1).

Experimental design

The experiment was established in late July 2007 in an abandoned cattle pasture located on the grounds of the secondary school of Nueva Palestina, in accordance with an agreement signed with the local authorities. This agreement aimed at educating students in native tree seedling production, as well as training local farmers in cost-effective methods of tree seedling establishment and maintenance activities before starting a forest restoration program in the community. Germination of seeds was carried out in a tree nursery established at the school. Seeds of 16 native tree species were collected from several adult fruiting trees between February and March of 2007. Exocarps were removed and seeds were planted within 10 days after collection. The upper soil layer (top 5 cm) of an adjacent mature forest was used as substrate. Seedlings were grown in a full sunlight environment during the subsequent four to six months in 15 x 25 cm black polyethylene bags and were approximately 25–40 cm tall when planted.

Approximately 10–15 days before seedling transplanting, all vegetation of the experimental area was cleared with a machete and burned to homogenize initial conditions. Site preparation did not include the use of fertilizers. A total of 960 seedlings of 16 species (60 individuals per species) were transplanted in the cleared area in 60 mixed plots, each measuring 8 x 8 m, covering a total area of 3,840 m^2. In each plot, 16 seedlings (one for each of the 16 species) were planted randomly at a 2 × 2–m spacing (Fig. 2). In the field, we observed a potential gradient of soil humidity. Therefore, the experiment was designed as randomized complete blocks with 15 replicates (each block containing four 8 × 8–m plots) in order to allow detection, during statistical analysis, of possible effects due to environmental variation. Four treatments of grass removal were randomly distributed within each block (Fig. 2).

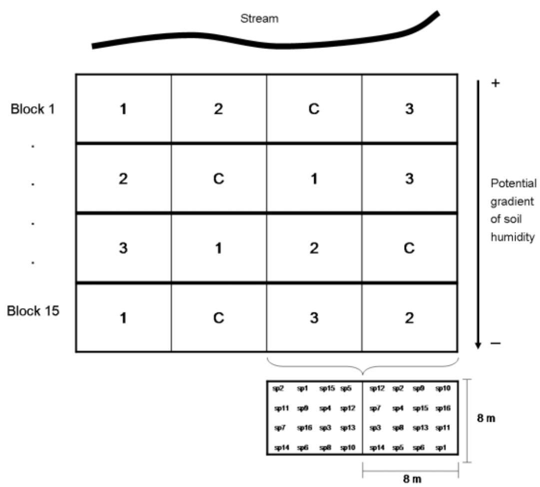

Fig. 2. Spatial arrangement of treatments and species in a complete randomized block design (C = Control, 1 = Treatment 1, 2 = Treatment 2, 3 = Treatment 3).

The control treatment included only the initial site preparation and no additional grass removal was done thereafter. In order to prevent the physical smothering of planted trees, grass removals were performed one meter around each tree at an interval of four months between treatments, time in which *C. plectostachyus* is capable of reaching 1.0–1.5 m height. Thus, treatment 1 plots received only one removal of grass four months after seedling transplant and no additional grass removal was done thereafter. Treatments receiving two (treatment 2) and three (treatment 3) grass removals were performed at four month intervals throughout the first year of establishment.

Field measurements and costs estimations

Maximum shoot height (m), basal stem diameter (cm), and tree survivorship (number of live individuals) were measured at age 7–10 days, and again 18 months after seedling transplant. Basal stem diameter was measured with calipers 5 cm above the root collar, and maximum shoot height was measured at the tip of the apical meristem with an extensible ruler.

Operational costs, materials, and labor requirements for activities related to plantation establishment and maintenance were also recorded for the entire study period. We estimated for each species the total costs associated with production of seedlings (tree nursery bags + seed recollection + substrate + nursery care), plantation establishment (site preparation + transportation of seedlings from the nursery to the experimental plots + seedling transplant), and maintenance (grass removals needed). These data were used to estimate the total plantation cost for each species on a per-hectare basis.

Data analysis

We calculated the survivorship for each species as the proportion of initially planted seedlings still alive 18 months after planting. As a means for comparing total species performance, we modified the integrated response index (IRI) previously used by [31, 32, 33] by combining seedling survival and above ground biomass (AGB) measurements as follows:

$$IRI = \text{survival proportion} \times (\ln AGB_{final} - \ln AGB_{initial}) \times (T_f - T_i)^{-1}$$

Where:

$AGB = (3.1416 \times BSD^2 \times H \times 4^{-1}) \times \rho$

BSD = Basal stem diameter (cm)

H = Height (cm)

ρ = Wood density ($g \times cm^{-3}$)

T = Time, final and initial (months)

We adapted the technical concept of risk [34] in order to introduce economics as a tool for the planning of restoration plantings by estimating more precisely the potential of establishing native tree seedlings in abandoned agricultural lands. We estimated a planting risk index (PRI) as follows:

$$PRI = \ln(\text{Total Plantation Cost}) \times IRI^{-1}$$

We tested for differences in survivorship, IRI and PRI separately by species, and by successional groups (in the case of PRI), as a function of grass removals, by using analysis of variance (ANOVA). When statistical differences were detected ($P < 0.05$), the Tukey multiple comparison procedure was performed in order to identify the most cost-effective grass removal treatment during early seedling establishment. We perform all statistical analyses and plots using SPSS version 15.0 (Prentice Hall Inc., New Jersey, U.S.A.).

Results

Seedling performance

The assumption of a potential effect of environmental heterogeneity was not supported, in the absence of statistically significant differences in species performance among blocks. Seedling survivorship of four of the 16 species studied was significantly affected by grass removals. The species *G. ulmifolia* ($F = 3.460$; $P = 0.022$), *E. folkersii* ($F = 3.717$; $P = 0.016$), *P. aquatica* ($F = 2.505$; $P = 0.069$), and *S. mombin* ($F = 3.963$; $P = 0.012$) showed better survivorship in response to more intensive treatments (Appendix 2). Half of all species planted showed at least 50% seedling survival. Survivorship of the species *O. pyramidale*, *Acacia* sp., *C. arborea*, and *P. sapota* was relatively low (25-50%), while the species C. *odorata*, *S. saponaria*, *Annona* sp., and *P. armata* showed poor seedling survival (less than 25%) at the end of the study period (Appendix 2).

Ten species showed statistically significant differences in IRI as a result of more intensive grass removals (Appendix 3). Notable examples were the species *G. ulmifolia* ($F = 50.171$; $P < 0.001$), *L. guatemalensis* ($F = 29.570$; $P < 0.001$), *M. calabura* ($F = 31.563$; $P < 0.001$), *O. pyramidale* ($F = 7.245$; $P = 0.001$), *A. mayana* ($F = 15.815$; $P < 0.001$), *E. folkersii* ($F = 28.671$; $P < 0.001$), *P. aquatica* ($F = 22.338$; $P < 0.001$), *S. mombin* ($F = 26.946$; $P < 0.001$), *T. rosea* ($F = 5.141$; $P = 0.001$), and *P. sapota* ($F = 10.354$; $P < 0.001$).

Species IRI was greatly improved in Treatment 3 (three grass removals at 4, 8, and 12 months), such as was detected for the species *L. guatemalensis*, *M. calabura*, *A. mayana*, *E. folkersii*, *P. aquatica*, and *S. mombin* (Appendix 3). Treatment 1 (one grass removal four months after plantation establishment) was found suitable for the species *G. ulmifolia*, *O. pyramidale*, *T. rosea*, and *P. sapota* (Appendix 3). Excepting the slow-growing species *P. aquatica* and *P. sapota*, all these species emerged over the pasture during the study period and showed a great potential to survive and shade-out grasses and facilitate natural regeneration in the subsequent years (Fig. 3).

Fig. 3. View of the experimental area at the end of the study period. Photo: F. Román-Dañobeytia.

Planting risk index (PRI) and costs estimates

PRI varied significantly among treatments within early-successional species (F = 10.014; $P < 0.001$) and mid-successional species (F = 6.286; $P < 0.001$). Late-successional species did not differ between treatments and showed PRI values 80% greater than those registered for early- and mid-successional species (Fig. 4). The PRI revealed that site preparation and plantation alone (control treatment) are not enough; at least one additional grass removal (Treatment 1) is required in order to assure acceptable seedling performance and reduce risk in *C. plectostachyus* abandoned pastures (Fig. 4).

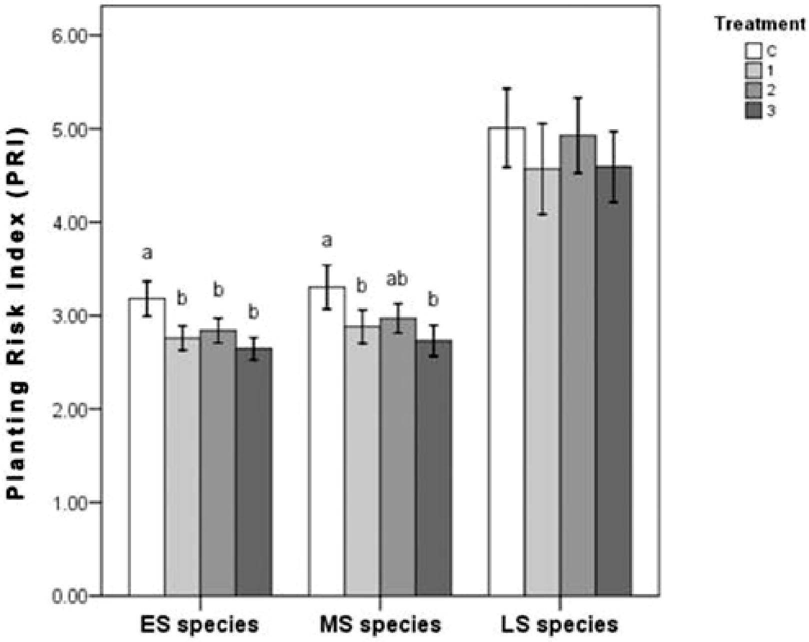

Fig. 4. Planting risk index (PRI) across treatments and successional groups (ES, early-successional; MS, mid-successional; LS, late-successional). Bars with different letters differ at *P* < 0.05 (ANOVA, Tukey test, *df* = 3).

Total seedling production, plantation establishment, and maintenance costs during the 1.5-year study period were close to US$ 1,260 per hectare (Table 1). Approximately, seedling production cost constituted 50% of the total plantation cost, while seedling transplant and grass control were 25% of the total cost, respectively. Based on our estimates, total costs were US$ 72 per hectare for early-successional species, US$ 74 for mid-successional species, and US$ 88 for late-successional species (Table 1). Costs of seedling production were higher for mid-, and late-successional species because of the scarcity of seeds for collection and/or the elevated high seed mass of certain species (e.g. *P. aquatica* and *P. sapota*). Furthermore, grass control costs were higher for late-successional species due to their slow growth and the need for controlling grasses for much longer (Table 1).

Table 1. Cost estimates of seedling production, plantation establishment, and grass control for the first 1.5 years of study[a]

	US$/ha		
	ES species	**MS species**	**LS species**
Seedling production costs			
Nursery bags	5.0	5.0	5.0
Substrate	5.67	5.67	5.67
Seed recollection	8.52	10.38	11.12
Nursery care	19.87	19.87	19.87
Subtotal	$39.06	$40.92	$41.66
Plantation establishment costs			
Site preparation	7.81	7.81	7.81
Transportation of seedlings	1.30	1.30	1.30
Seedling transplant	11.72	11.72	11.72
Subtotal	$20.83	$20.83	$20.83
Grass control costs			
Subtotal	$13.08 (T1)*	$13.08 (T1)*	$26.16 (T3)*
Total costs	$291.88 (x 4 spp)	$523.81 (x 7 spp)	443.25 (x 5 spp) $1258.94 (x 16 spp)

[a] During the period of study, 1 US$ = 12.0 Mexican pesos. ES, early-successional; LS, late-successional; MS, mid-successional.
* Treatments were assigned on the basis of Fig. 4.

Discussion

Effect of grass removals on seedling performance

The different intensities of grass removal used in this experiment revealed different management options, in terms of their cost-effectiveness, for establishing tree seedlings in abandoned pastures. Grass removals generally improved the sapling performance of a range of native tropical tree species and greatly reduced *C. plectostachyus* dominance even if it did not lead to eradication. The application of only one grass removal four months after planting (Treatment 1) could be sufficient for certain fast-growing species in *C. plectostachyus* abandoned pastures, especially when funds for establishing restoration plantings are limited. Nonetheless, many species continued to respond positively to more frequent cleanings, thereby Treatments 2 and 3 could be appropriate in order to achieve socioeconomic and restoration goals more rapidly when funds are not restricted.

These results agree with other studies of tree seedling development in abandoned tropical pastures dominated by non-native invasive grasses, such as *Hyparrgenia rufa* in Costa Rica [22], *Pennisetum setaceum* in Hawai'i [35], and *Saccharum spontaneum* in Panama [24]. Survival and growth rates of tree species always increased significantly with more intense grass removal treatments, and trees receiving less frequent treatments suffered greater mortality and lower growth. However, the intensity of grass control treatments could vary depending on the competitive ability of the grass species to be controlled. Also, a few studies have suggested that grass control during the dry season could be stressful for seedlings, especially in clay-like soils exposed to direct sunlight and subject to cracking [36, 37]. Nonetheless, maintaining high amounts of grass biomass in the dry season also increases fire risks [38]. This kind of trade-off is a subject that requires further research.

Planting risk index (PRI) and costs estimates

Our results suggest that PRI can be minimized in abandoned pastures by planting a higher density of light-demanding and fast-growing early- and mid-successional species relative to shade-tolerant and slow-growing late-successional species. This strategy may have the potential to reduce the cost and need for grass control by encouraging early plantation crown closure, as well as to assist natural tree species regeneration [39, 17, 18, 19]. However, in view of their long-term contribution to forest restoration, it is important to select carefully late-successional species with potential to be acclimatized in open areas [9, 40]. Even though initial survivorship might be low, the possibility of a few individuals of late-successional species surviving and becoming large trees sufficiently merits their inclusion in restoration plantings. In our study this could be possible for *Acacia* sp., *C. arborea*, and *P. sapota*, which showed survival rates ranging from 25% to 50%. Depending on the landscape context and the proximity to mature forest fragments [41], another option is to perform enrichment plantings or direct seeding of late-successional species once the canopy closes on a plantation comprised mostly of early- to mid-successional species [42].

Total costs of plantation establishment were different depending on the type of species. For example, costs of seed recollection were lower for early-successional in comparison to mid- and late-successional tree species. Trees of early-successional species produce many seeds per plant each year, they can be found in close proximity to villages, and their seeds are easily collected. In contrast, trees of mid- and late-successional species do not produce fresh seeds every year, are generally located in mature forests far away from villages, and seeds are more difficult to collect because of their high seed mass [43, 44]. Time and effort are also higher for controlling grasses around slow-growing late-successional species than for fast-growing early- and mid-successional species. Therefore, proper species arrangement in plantations can improve overall plant performance through complementarity and facilitation interactions between species [e.g. 19, 9]. The assessment of a planting risk index for each species across a variety of environmental circumstances may also help land managers to match species with planting sites accurately.

Estimates of total plantation establishment costs in the Lacandon region were close to US$ 1,260 ha^{-1}, based on a 2 × 2–m spacing grid (2,500 trees planted ha^{-1}). However, it may increase to US$ 1,610–1,820 ha^{-1} if payments for technical monitoring personnel are included. These costs are favorable compared with those for plantation establishment using nursery-grown seedlings in other tropical regions. For example, in the Panama Canal Watershed, it was reported that total plantation costs for two timber species averaged US$ 1,590–2,570 ha^{-1} in year 1, using a 3 × 3–m spacing grid (1,111 trees planted ha^{-1}) [24]. In the Brazilian Atlantic Forest, costs of plantation establishment of a high diversity (> 80 species) of native trees ranged from US$ 3,000 to 4,500 ha^{-1} with a planting density of 2 x 3–m (1,666 trees planted ha^{-1}) [19].

Forest restoration is becoming more important worldwide because of the possibility of reconciling profitable land use with biodiversity conservation goals and the provision of ecosystem goods and services to society at large [2, 3]. However, for the time being, it is clear that legal incentives and economic support will be needed to assist restoration interventions, starting with seed collecting and nursery costs [45], and extending right though to planting and post-planting site maintenance such as the grass removals described here. Legal instruments that encourage environmental certification for industries appear to be helpful for funding forest restoration activities in some countries [46, 47], while valuation through trade and sales promotion of certified forest products, and rewards for ecosystem services rendered (including carbon sequestration) can also help to expand forest restoration in rural poor communities of the tropics and in more extensive areas [6, 1].

Implications for conservation

Grass control around transplanted seedlings is a viable, low-cost approach for reintroducing native tree species that are difficult to establish naturally into abandoned tropical pastures. Grass removals could reduce the species planting risk by improving seedling performance significantly. Although many species continued to respond positively to more grass removals, the extent of restoration possible through this method will be determined by the availability of economic resources. The planting risk index can also be minimized in abandoned pastures by planting higher densities of early- and mid-successional species, relative to late-successional species. However, late-successional species are key in restoration actions as they promote long-term ecosystem functioning. Therefore, it is important to re-test more species of the same successional group in abandoned agricultural lands and/or in the understory of restoration plantings and secondary forests. Given the variability in species performance and total plantation costs, conducting a planting risk analysis prior to major investments could help land managers to improve the efficiency and effectiveness of large-scale, long-term restoration programs.

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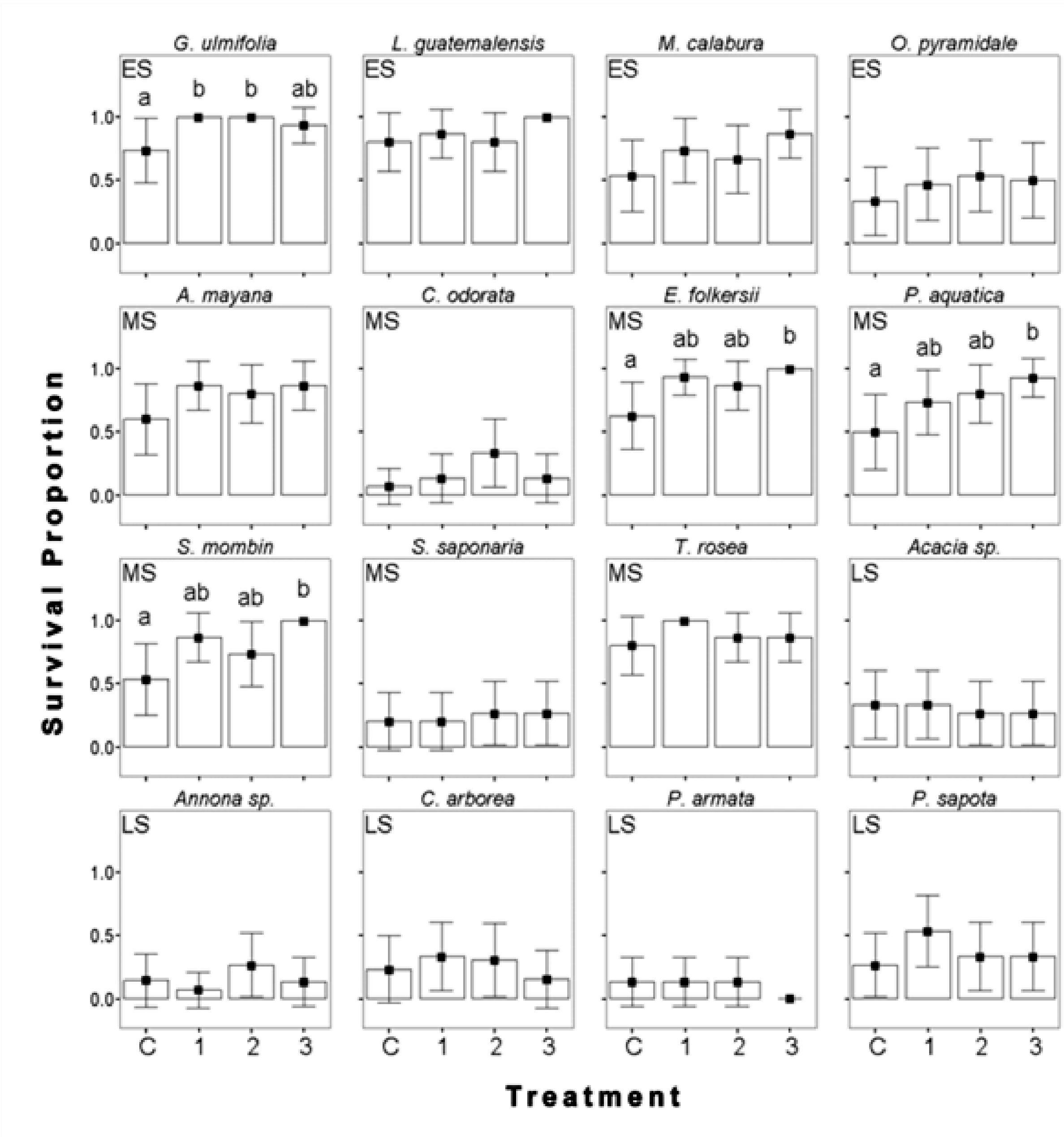
Appendix 1. Botanical families, ecological, structural, and ethnobotanical characteristics of 16 tropical native rainforest tree species used in the present study.

Species	Family[a]	Successional status[b]	Adult height[c] (m)	Wood density[d] (g/cm^3)	Uses[c]
Guazuma ulmifolia Lam.	Malvaceae	ES	2 – 20	0.51	Fodder, fuelwood
Lonchocarpus guatemalensis Benth.	Fabaceae	ES	10 – 20	0.73	Fuelwood, timber
Muntingia calabura L.	Muntingiaceae	ES	10 – 12	0.3	Fruit, fiber (bark)
Ochroma pyramidale (Cav. ex Lam.) Urb.	Malvaceae	ES	20 – 25	0.14	Handicraft, timber
Acacia mayana Lundell	Fabaceae	MS	2 – 6	0.73	Fruit
Cedrela odorata L.	Meliaceae	MS	25 – 35	0.46	Timber
Erythrina folkersii Krukoff & Moldenke	Fabaceae	MS	5 – 16	0.38	Fodder, handicraft
Pachira aquatica Aubl.	Malvaceae	MS	15 – 18	0.38	Timber
Sapindus saponaria L.	Sapindaceae	MS	12 – 15	0.67	Soap (fruit), timber
Spondias mombin L.	Anacardiaceae	MS	18 – 20	0.39	Fruit, timber
Tabebuia rosea (Bertol.) A. DC.	Bignoniaceae	MS	20 – 25	0.52	Timber
Acacia sp.	Fabaceae	LS*	20 – 25	0.67	Timber
Annona sp.	Annonaceae	LS*	15 – 20	0.44	Fruit, timber
Cojoba arborea (L.) Britton & Rose	Fabaceae	LS	25 – 30	0.61	Timber
Poulsenia armata (Miq.) Standl.	Moraceae	LS	20 – 25	0.38	Timber, fiber (bark)
Pouteria sapota (Jacq.) H.E. Moore & Stearn	Sapotaceae	LS	35 – 40	0.9	Fruit, timber

[a] http://www.tropicos.org; [b] Adapted from [30]; ES, early-successional; LS, late-successional; MS, mid-successional.
[c] [27]; [d] http://hdl.handle.net/10255/dryad.235; * *Acacia* sp. “kuban” and *Annona* sp. “omash” are recognized as mature forest species by the Maya-Lacandon indigenous people.

Appendix 2. Species survivorship across four intensities of grass removal 18 months after planting. Bars with different letters differ at $P < 0.05$ (ANOVA, Tukey test, $df = 3$). Survival proportion was arcsin transformed prior to statistical analysis in order to comply with normality assumptions. ES, early-successional; MS, mid-successional; LS, late-successional.



Appendix 3. Species total performance across four intensities of grass removal 18 months after planting. Bars with different letters differ at $P < 0.05$ (ANOVA, Tukey test, $df = 3$). ES, early-successional; MS, mid-successional; LS, late-successional.