Direct seeding of late-successional trees to restore tropical montane forest

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A B S T R A C T

Natural regeneration of large-seeded, late-successional trees in fragmented tropical landscapes can be strongly limited by a lack of seed dispersal resulting in the need for more intensive restoration approaches, such as enrichment planting, to include these species in future forests. Direct seeding may be an alternative low-cost approach to planting nursery-raised tree seedlings, but there is minimal information on its efficacy or when in the successional process this technique will be most successful. We tested directly seeding five native tree species into habitats representing passive and active restoration approaches: (1) recently abandoned pasture; (2) naturally establishing, young secondary forests; and (3) young, mixed-species (fast-growing N-fixers and commercially valuable species) tree plantations established to facilitate montane forest recovery in southern Costa Rica. We monitored germination, survival, growth, and above- and below-ground biomass over a 2-year period. Germination in pastures, secondary forests, and tree plantations was similar (~43%). Seedling survival after one and two years was significantly higher under tree plantations (91% year 1, 75% year 2) compared to secondary forests (76, 44%) or pastures (74, 41%). Moreover, seedlings had greater total biomass and lower root:shoot ratios in the plantations, suggesting higher nutrient availability in that treatment. Costs for direct seeding were 10- to 30-fold less per 100 seedlings after 2-year compared to nursery-raised seedlings planted at the same sites; however, there are important trade-offs to the two restoration approaches. Planting nursery-raised seedling is a more effective but higher cost approach for rapidly establishing canopy cover and restoring large areas whereas direct seeding is a more efficient way to enrich an existing system. We particularly recommend using direct seeding as a complimentary measure to the more intensive restoration approach of planting fast-growing and N-fixing trees.

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1. Introduction

Natural regeneration of late-successional trees in fragmented and degraded landscapes can be strongly limited by a lack of seed dispersal into successional habitats (e.g. Duncan and Chapman, 1999; Holl, 1999; Rodrigues Da Silva and Matos, 2006; Wijdeven and Kuzee, 2000); this limitation is particularly acute for larger-seeded animal-dispersed trees. Studies across a range of locations in the tropics show that movement of larger seeds beyond the edges of forest fragments is rare (Cole, 2009; del Castillo and Rios, 2008; Dosch et al., 2007; Duncan and Chapman, 1999; Holl, 1999; Ingle, 2003) and establishment of these species in natural regeneration is limited even after many decades of succession (Aide et al., 2000; Finegan, 1996). The lack of natural recruitment of these species has led to concerns over their persistence in fragmented and degraded landscapes, and more aggressive restoration efforts such as enrichment planting have been suggested as a necessary step to augment severely dispersal-limited species in future forests (e.g. Dosch et al., 2007; Martinez-Garza and Howe, 2003; Zimmerman et al., 2000).

The predominant method used to restore degraded tropical lands is to plant nursery-raised tree seedlings (Chazdon, 2008; Lamb et al., 2005). Although this can be an effective technique for quickly establishing forest cover (Holl et al., 2010; Montagnini, 2001; Wishnie et al., 2007), there are drawbacks that make this method less useful for the restoration of most mature-forest species. First, the selection of species available from nurseries is often limited to trees that have commercial or agricultural value, and for which propagation techniques are known (Sautu et al., 2006). Second, studies of the seed biology of mature-forest trees suggest that a majority of larger-seeded species are recalcitrant (sensitive to desiccation and temperature, and germinate rapidly; Daws et al., 2005; Sautu et al., 2006; Vazquez-Yanes and

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Orozco-Segovia, 1990) making them difficult to store or establish in nurseries. Finally, planting nursery-raised seedlings can be quite costly and labor intensive (Engel and Parrotta, 2001; Hardwick et al., 1997; Zahawi and Holl, 2009) particularly when it involves the use of native species about which little is known (Blakesley et al., 2002; Sautu et al., 2006).

One potential alternative is to collect seed from local sources and plant them directly into the habitats targeted for restoration. Although direct seeding has not been widely adopted in forestry practice, it has been successfully used for establishment of some tropical and subtropical tree crops such as *Acacia*, *Anacardium occidentale*, *Gmelina arborea*, and *Pinus* (Engel and Parrotta, 2001; Evans, 1982). Only a handful of studies, however, have tested directly seeding late-successional, large-seeded trees as a restoration strategy (Bonilla-Moheno and Holl, 2009; Camargo et al., 2002; Doust et al., 2006; Hooper et al., 2002) and there is a need for better information on the habitat types and stage of succession in which direct seeding can be applied effectively.

The few previous direct seeding studies suggest that it is a promising restoration strategy for larger-seeded tree species (Camargo et al., 2002; Doust et al., 2006; Hardwick et al., 1997; Hooper et al., 2002; Nepstad et al., 1991) but results among habitat types have generally yielded divergent trends. For example, Hooper et al. (2002) found that larger-seeded, shade tolerant trees successfully germinated and grew under *Saccharum* pasture grasses in Panama, whereas Sampaio (2007) reported low levels of establishment from seeds planted into pastures in seasonal deciduous forest in Brazil. Camargo et al. (2002) reported that larger-seeded species could grow on degraded, bare ground and in pasture, but that seedlings survived less well in successional and mature forest in the Central Amazon. Conversely, Bonilla-Moheno and Holl (2009) found similar levels of survival and growth in 8–15 years and >50-year-old forests in the Yucatan but two of the three species (*Brosimum alicastrum* Sw., *Enterolobium cyclocarpum* (Jacq.) Griseb. compared to *Manilkara zapota* (L.) Royen) performed less well in recently abandoned (<5 years) fields. Other authors have suggested introducing a mixture of seedlings and seeds, or introducing later-successional species after a canopy of early-successional species has been established (e.g. Camargo et al., 2002; Hardwick et al., 1997; Ray and Brown, 1995). Thus far, it is not clear whether direct seeding can be usefully applied in both early and later stages of succession or used as a supplementary step in more intensive restoration planting. Finally, although direct seeding is often considered to be a low-cost approach (see Engel and Parrotta, 2001), there have been few actual cost comparisons between direct seeding and planting seedlings in a restoration setting.

The goal of this study was to evaluate the potential of direct seeding under a range of possible restoration settings. We planted seeds of five, large-seeded, late-successional trees into three habitat types that represented different successional stages and restoration approaches: in recently abandoned pasture; under naturally established young (8–10 years) successional forest; and under 3-year-old tree plantations established to facilitate tropical forest recovery. Specifically, we aimed to (1) assess how planting seeds into different successional stages and restoration treatments affected seed germination and seedling establishment, survival, and growth, and (2) compare the logistics and costs of direct seeding using locally collected seeds with planting nursery-raised seedlings.

2. Methods

2.1. Study area

The study was carried out at sites spread between the Las Cruces Biological Station (8°47′7″N, 82°57′32″W) and the town of Agua Buena (8°44′36″N, 82°58′04″W) in Coto Brus County in southern

Costa Rica. The forest in this region is classified as a tropical montane rain forest by Holdridge et al. (1971). Study sites range from 1110 to 1290 m a.s.l. and the mean annual rainfall is *ca.* 3500 mm with a distinct dry season from December to March. The soils are a mix of ultisols and andisols, and the topography of the area is mountainous with much of the former agriculture land located on steeply sloping (15–40°) land.

Prior to 1950, the region was largely forested but over the last 60 years all but ∼25% of the forest was cleared for agriculture (Daily et al., 2001). As is typical throughout much of Central America, the landscape is a highly fragmented mosaic of small remnant forests, patches of active agriculture, fallow plots, and pasture. Between 1990 and 2002, changes in the global coffee market led to extensive conversion of coffee plantations to pasture and the fallowing of marginal agricultural lands, resulting in numerous patches of young successional forests (Rickert, 2005). Because most primary-forest fragments are protected under Costa Rica's forestry laws, conservation efforts in the region focus on reforestation and restoration of degraded lands.

2.2. Species selection

We selected five large-seeded primary-forest tree species based on the fruiting cycles of local trees, and the availability of sufficient quantities of seed at the time of the study (Table 1). From March through August 2007, we regularly checked the four largest primary-forest fragments near the restoration sites for fruiting trees, and consulted with local tree nurseries and farmers' cooperatives regarding information on the locations and fruiting times of seed-bearing trees. Seeds of three species (*Ruagea glabra*, *Otoba novogranatensis*, and *Garcinia intermedia*) were collected exclusively within a 10-km radius of planting sites, whereas two species (*Pseudolmedia spuria* and *Calophyllum brasiliense*) were collected in part near the Las Alturas Biological Station (8°56′43″N, 82°50′00″W), a non-fragmented reserve of more than 10,000 ha ∼25 km away. In all cases, we were able to gather freshly fallen seeds from beneath at least four widely separated parent trees. Collected seeds were mixed and stored for ≤3 days before being soaked for 12–24 h to imbibe water prior to planting. We discarded all seeds that showed signs of damage or floated in water (Schatral and Fox, 1994). These species are referred to by their generic names throughout.

2.3. Experimental design

We seeded into four replicate blocks containing three habitat types: experimentally established native tree plantations (3 years since tree planting); recently abandoned pasture (3 years since grazing), and secondary forest (8–10 years since agriculture or grazing). All sites were separated by ≥0.5 km and were previously used for a mixture of coffee and pasture. The plantation and pasture treatments were established in 50 m × 50 m plots in 2004 as part of a large-scale restoration research project to test the effects of different tree planting strategies on forest recovery (described in detail in Cole et al., 2010). The study was set up in a randomized-block design and therefore pairs of these treatments were located adjacent to each other (10–50 m distance between plots). The randomized-block design was used to place groups of treatments in areas with similar land use histories and microclimates as these varied highly across the landscape (see Holl et al., 2010 for site details).

We maintained this design by selecting the nearest secondary forest to each plantation–pasture pair that met our criteria (8–10 years growth and similar previous land use to other treatments): all secondary forests were within ∼20–200 m of the other treatments in a block.

Table 1
Tree species, seed weight, number of seed per treatment, common collection techniques, and seed and species characteristics.

Species	Fresh wt (g)	Seeds per treatment	Month planted	Collection, seed characteristics, and treatment	Species characteristics
Calophyllum brasiliense Cambess [Clusiaceae]	3.0 ± 0.6	384	June	Collect from ground or tree, recalcitrant, soak 24 h	Late-successional mid-canopy tree. Commercially valuable wood, harvested for furniture and construction
Garcinia intermedia (Pittier) Hammel [Clusiaceae]	1.8 ± 0.3	576	May	Collect from ground or tree, seed subject to rapid desiccation, no treatment	Lower canopy tree. Occasionally cultivated as ornamental and for fruit
Otoba novogranatensis Moldenke [Myristicaceae]	4.6 ± 0.8	768	April	Collect from ground, recalcitrant, no treatment	Canopy late-successional. Used for construction, some medicinal and cosmetic uses
Pseudolmedia spuria (Sw.) Griseback [Moraceae]	1.9 ± 0.4	576	June	Collect from ground, soak 24 h	Canopy tree, commercially valuable wood
Ruagea glabra Vahl [Meliaceae]	2.7 ± 0.5	576	March	Collect from ground, recalcitrant, soak 24 h	Canopy tree, shade tolerant, wood used for construction, furniture

Plantation plots were established using nursery-raised seedlings of four tree species. Two native species, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), are commercially valuable timber species, have been shown to establish well on degraded soils in the region (Carpenter et al., 2004a), and exhibit rapid growth in forestry trials of native species (Van Breugel et al., 2010). Two species, *Erythrina poeppigiana* (Walp.) O.F. Cook and *Inga edulis* Mart. (both Fabaceae), are fast-growing, naturalized N-fixing species commonly used in agriculture. At the initiation of this study, plantations had developed closed canopies (overhead cover 91–96%), grass cover had been largely eliminated, and ground cover consisted of sparse ruderal herbs and leaf litter (bare ground 50–75%; Zahawi et al., unpublished data).

Vegetation in the pasture and plantation treatments was cleared to ground level by machete every ~2.5 months until December 2006 to allow planted seedlings to establish and to maintain similar conditions between treatments. Clearing ceased ~3 months prior to the initiation of this study in 2007. At the start of the study, pasture plots were dominated by several introduced forage grasses, primarily *Axonopus scoparius* (Flugge) Kuhlm., *Paspalum* spp. and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R. D. Webster, and ruderal herbs and ferns, such as *Heterocondylus vitalbae* (D.C.) King & H. Robins., *Pteridium arachnoideum* (Kaulf.) Maxon, and *Spermacoce assurgens* Ruiz & Pav. Overhead cover and bare ground were low (both 0–5%) (Zahawi et al., unpublished data). Percent soil moisture at the end of the dry season (March 2008) was similar in pastures and plantations (14.3 ± 0.7) (Loik, unpublished data).

Secondary forest patches (~1–3 ha in size) were cleared originally to grow coffee and two of the sites were later used for pasture. To standardize the plot size, we marked a 50 m × 50 m plot in the center of each secondary forest. The structural characteristics of the secondary forests were relatively heterogeneous. Canopy height ranged from 5 to 15 m, overhead cover varied from 45 to 90%, and stem density (dbh ≥2 cm) ranged from 1406–6875 stems/ha. Ground cover was sparse and herbaceous vegetation included commonly occurring species such as *Teliostachya alopecuroidea* (Vahl) Nees, *Monnina xalapensis* var. *xalapensis* Kunth, *Vernonia arborescens* (L.) Sw., *Heliconia latispatha* Benth and *Piper* spp. Bare ground was 10–25%. Dominant tree species included *Cecropia obtusifolia* Bertol., *Conostegia xalapensis* (Bonpl.) D. Don ex DC., *Croton draco* Schltdl., *Heliocarpus appendiculatus* Turcz., and *Psidium guajava* L. (Cole, unpublished data). We did not find any large N-fixing trees in these experimental plots.

Within each 50 m × 50 m plot, we established three 5 m × 8 m subplots separated by a minimum of 10 m. All data from the three subplots were combined and the plot was considered a replicate ($n = 4$/treatment). To prepare areas for planting, we cut above-ground grass and herbaceous vegetation in each subplot to ground level. All trees, saplings, and shrubs were left standing since the objective of the study was to evaluate enrichment seeding under existing woody and successional vegetation. Each subplot was divided into five 1 m × 8 m areas within which we planted seeds of a single species in two rows at a depth of ~3 cm. At sites where there was a layer of litter (plantations and secondary forests) the litter was pushed to one side of the planting rows so seeds could be placed in mineral soil. Planting density ranged from 4 to 8 seeds m^{-2} depending on the quantity of seed collected. Ninety-six to 192 seeds were planted per replicate habitat and all planting was carried out between 1 March and 15 June 2007 (Table 1). Grasses and herbaceous vegetation in the pasture treatments was cut every 3 months to a height of 0.5 m using a machete for the first year, in order to reduce light competition for seedlings and to facilitate data collection. No maintenance was necessary in plantations or secondary forests as there was minimal grass and herbaceous cover in the understory.

2.4. Data collection

We monitored germination monthly for the first three months following planting, thereafter at ~3 months intervals to 1 year, and again at the end of the second year. Survival of germinated seeds was recorded at 12 and 24 months following planting. Between June 15 and July 10, 2008, after approximately 1 year of growth after planting, we recorded seedling height to the nearest cm by measuring the distance between the soil surface and the tip of the terminal meristem. At this time we also harvested a subset of seedlings to measure total above- and below-ground biomass and collect leaves for foliar nutrient analyses. Due to the labor-intensive nature of collecting below-ground biomass, five seedlings of each species per replicate plot were harvested for a total of 60 seedlings per species with one exception: in two plots only four seedlings of *Calophyllum* were collected due to low germination. Seedling survival in year 2 was calculated as the percentage of those that survived after biomass harvesting.

We collected above-ground biomass from randomly selected seedlings by clipping the stems of the seedlings at ground level. We carefully excavated the root system using small spades, kitchen utensils, and fingers. The roots of each seedling were thoroughly washed to remove soil, and above- and below-ground biomass were determined after drying samples at 65 °C for 24–48 h. Leaves from the ~5 seedlings/species/replicate were bulked, ground with a Wiley mill and analyzed for nutrients at Brookside Laboratories, Knoxville, OH. Nitrogen was measured by combustion with an elemental analyzer; other nutrients were analyzed on a Thermo Jarrell Ash ICP (Thermo Fisher Scientific, Waltham, MA) after microwave

digestion with nitric acid and hydrogen peroxide (Gavlak et al., 2003).

We collected five 2.5-cm diameter × 15-cm deep soil cores from each subplot (for a total of 15 per whole plot) in July 2008. The 15 cores per plot were mixed, passed through a 2-mm sieve, air dried, and analyzed for organic matter, Bray P, and micronutrients following standard procedures at Brookside Laboratories (Gavlak et al., 2003). We also collected three soil bulk density samples from each subplot (for a total of nine per replicate) using a 4-cm diameter × 10-cm depth core. Bulk density samples were dried at 105 °C for ≥48 h and weighed.

2.5. Costs and logistics

To estimate costs, we averaged our search, collection, and processing time for each 100 seeds. We then followed the methods Zahawi and Holl (2009) used to calculate establishment costs for the nursery seedlings used for the experimental tree plantations: we calculated labor hours for clearing and planting, post-planting field maintenance, fuel and transportation per 100 seedlings surviving at year 2 in each habitat type. We used a generic salary of $1/hour to calculate labor expenses following Zahawi and Holl (2009).

2.6. Statistical analyses

We used randomized-block two-way analyses of variance (ANOVA) to compare the effects of habitat and species and their interactions on percent germination, percent of seeds surviving as seedlings after 1 and 2 years, seedling height, total biomass, root:shoot ratio, and foliar nutrients. Seedling survival in year 1 and year 2 were analyzed separately because (a) survival in year 2 was estimated from the percent of seedlings surviving after some were harvested for biomass, and (b) data from one block were not used in year 2 after the secondary forest was cleared for agriculture and cows broke through the fence and trampled seedlings in the pasture plot. Soil nutrients and bulk density were compared among habitats using randomized-block one-way ANOVAs. We tested the relationship between soil and leaf chemical parameters using Spearman rank correlation coefficients. We also tested the relationships between overall percent germination, percent surviving at year 1, seedling height, total biomass and root:shoot ratio to soil and foliar nutrients using Spearman rank correlation coefficients.

Percentage variables were arcsine square root transformed and some variables were log + 1 transformed or ranked in order to meet assumptions of normality and homogeneity of variances (Zar, 1996). Post hoc analyses for pair-wise comparisons of means were undertaken using Tukey's HSD test ($p = 0.05$). We report means ± 1 SE throughout. All analyses were conducted using Systat 12.0 (SYSTAT Software Inc.) and all ANOVA's followed the GLM procedure.

3. Results

3.1. Germination and survival

Of the 8880 seeds planted, 43% germinated and of these 87% survived as seedlings by the end of the first year. A total of 64% of germinated seeds (not including the seedlings that were harvested for measurements in year 1) survived as seedlings by the end of the second year. Percent germination varied significantly among species ($F = 17.8$, df = 4, $p < 0.0001$) but not across habitat types ($F = 2.3$, df = 2, $p < 0.1086$), and there were no interaction effects ($p > 0.05$; Fig. 1). *Garcinia* had the highest germination (90%); germination of the remaining four species ranged between 25 and 37% (Table 2).

Seedling survival varied strongly by both habitat and species (but there were no habitat × species interactions). Significantly
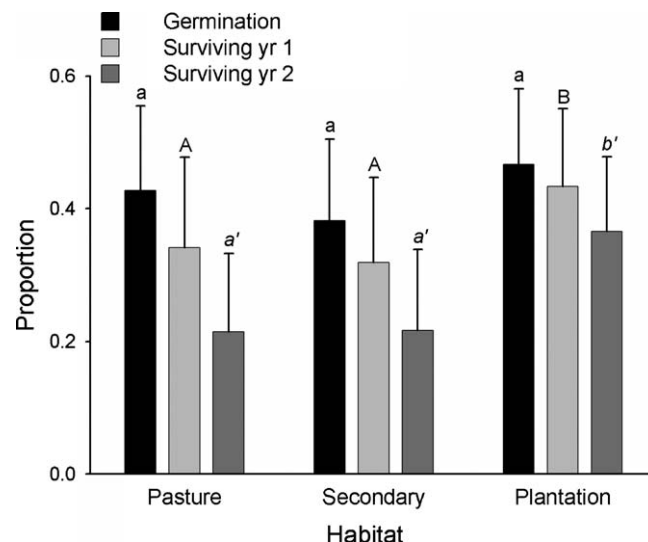

Fig. 1. Proportion of seeds (averaged across all species) that germinated and survived as seedlings one and 2* years after planting in each of three habitats. Error bars are means ± SE. Means with the same letter are not significantly different among habitat types ($p > 0.05$) using Tukey's HSD. *The values for year 2 are calculated from the percent of surviving seedlings after some were harvest for biomass at the end of year 1 and are from 3 replicate blocks; all other measurements are from 4 replicate blocks.

more germinated seeds survived as seedlings in the plantations as compared to both secondary forests and pastures by the end of year 1 ($F = 7.6$, df = 2, $p = 0.0015$) and year 2 ($F = 18.3$, df = 2, $p < 0.0001$); secondary forests and pastures did not differ. Among species, *Garcinia* had significantly higher overall survivorship in year 1 ($F = 6.1$, df = 4, $p = 0.0005$) and year 2 ($F = 8.3$, df = 4, $p < 0.0001$) compared to the other four trees, which were similar to each other (Table 2).

Table 2
Percent of seeds germinating and surviving as seedlings at year 1 and year 2[a] ± SE are shown for the five tree species in each habitat type. Totals among the species in each category with the same letters are not significantly different ($p > 0.05$) using Tukey's HSD.

Species	Habitat			Totals
	Pasture	Secondary	Plantation	
C. brasiliense				
Germination	30.0 ± 5.2	19.3 ± 3.0	28.2 ± 3.1	25.8 ± 2.5a
Surviving year 1	29.5 ± 1.9	19.3 ± 4.0	23.0 ± 2.4	17.6 ± 2.2a
Surviving year 2	9.7 ± 0.3	4.0 ± 0.5	20.0 ± 1.7	11.2 ± 2.4a
G. intermedia				
Germination	94.1 ± 3.7	84.5 ± 4.2	90.1 ± 3.7	89.8 ± 2.1b
Surviving year 1	88.5 ± 4.0	81.0 ± 4.0	88.2 ± 3.6	85.9 ± 2.3b
Surviving year 2	69.3 ± 6.7	68.0 ± 2.1	79.7 ± 7.4	72.3 ± 3.5b
O. novogranatensis				
Germination	31.2 ± 3.5	29.8 ± 3.1	30.8 ± 1.9	30.6 ± 1.5a
Surviving year 1	22.5 ± 3.3	24.0 ± 3.3	27.5 ± 2.7	24.7 ± 1.8a
Surviving year 2	9.7 ± 1.7	13.0 ± 1.0	24.7 ± 1.8	15.8 ± 2.4a
P. spuria				
Germination	25.8 ± 6.7	17.5 ± 3.2	44.0 ± 1.0	29.1 ± 5.0a
Surviving year 1	20.8 ± 6.7	13.8 ± 4.2	40.5 ± 9.5	25.0 ± 5.1a
Surviving year 2	14.3 ± 6.2	7.0 ± 3.5	22.0 ± 4.1	14.4 ± 3.2a
Ruagia glabra				
Germination	32.5 ± 11.7	40.0 ± 1.6	40.0 ± 8.6	37.4 ± 6.5a
Surviving year 1	13.8 ± 4.2	34.3 ± 1.5	37.5 ± 8.6	30.5 ± 6.4a
Surviving year 2	9.7 ± 1.1	10.0 ± 5.0	26.7 ± 1.2	15.4 ± 4.1a

[a] The percent surviving to year 2 is of seedlings remaining after some seedlings were harvest for biomass at the end of year 1 and are from 3 replicate blocks. All other measurements are from 4 replicate blocks.

Table 3

Mean foliar nutrient concentrations by habitat. Means with the same letter are not significantly different ($p > 0.05$) using Tukey's HSD. Bracketed values are the maximum and minimum range of concentrations.

Nutrient	Pasture	Secondary forest	Plantation
N (%)	1.19 ± 0.09^a (0.7–2.2)	1.23 ± 0.07^a (0.7–1.9)	1.96 ± 0.93^b (1.4–2.7)
P (%)	0.11 ± 0.02^a (0.1–0.3)	0.10 ± 0.10^a (0.1–0.2)	0.14 ± 0.01^b (0.1–0.2)
K (%)	1.28 ± 0.10^a (0.6–2.0)	1.13 ± 1.04^a (0.4–2.3)	1.24 ± 0.10^a (0.7–1.9)
Ca (%)	1.04 ± 0.11^a (0.5–2.1)	1.07 ± 0.14^a (0.3–1.4)	1.11 ± 0.11^a (0.5–2.2)
Mg (%)	0.31 ± 0.03^a (0.1–0.6)	0.29 ± 0.02^a (0.1–0.5)	0.31 ± 0.02^a (0.1–0.5)
S (%)	0.14 ± 0.01^a (0.1–0.2)	0.12 ± 0.01^b (0.1–0.2)	0.17 ± 0.01^c (0.1–0.3)
B (mg kg^{-1})	40.4 ± 3.8^a (15–87)	43.0 ± 6.3^a (17–122)	42.3 ± 3.9^a (20–83)
Al (mg kg^{-1})	753.3 ± 53.1^a (400–1134)	900.0 ± 105.3^a (296–1919)	615.1 ± 58.2^b (139–1230)
Fe (mg kg^{-1})	441.9 ± 40.9^{ab} (169–730)	718.2 ± 205.9^b (99–4219)	381.6 ± 41.7^a (92–821)
Mn (mg kg^{-1})	202.3 ± 33.7^a (37–504)	192.6 ± 46.3^{ab} (30–890)	192.6 ± 40.0^b (27–657)
Cu (mg kg^{-1})	$11.4 \pm 0.8a^a$ (5–18)	13.5 ± 1.35^a (7–28)	17.6 ± 1.3^b (8–30)
Zn (mg kg^{-1})	33.0 ± 4.3^b (14–90)	22.1 ± 1.5^a (13–33)	28.0 ± 1.6^b (19–42)

3.2. Height and biomass

Mean seedling height was significantly greater in plantations (17.9 ± 1.5 cm) compared to secondary forests (12.4 ± 0.9) and pastures (13.9 ± 0.7; $F = 26.9$, df = 2, $p < 0.0001$). Seedling height varied greatly among species ($F = 51.7$, df = 4, $p < 0.0001$), with *Ruagea* growing the most (18.7 ± 1.7 cm) and *Pseudolmedia* the least (9.9 ± 0.7).

Height and biomass were significantly positively correlated in all habitats ($p < 0.05$, $r^2 > 0.50$); however, the trends in growth differed slightly between these measurements. Total biomass varied among all of the habitats ($F = 16.8$, df = 2, $p < 0.0001$). Seedlings in plantations had the greatest total biomass (2.8 ± 0.7 g); secondary forests were intermediate (1.4 ± 0.2 g), and pastures lowest (1.0 ± 0.1 g; Fig. 2). Similarly, root:shoot ratio was highest in pastures (1.0 ± 0.1), intermediate in secondary forest (0.8 ± 0.1), and lowest in plantations (0.5 ± 0.0; Fig. 2, $F = 53.4$, df = 2, $p < 0.0001$). Not surprisingly, biomass and root:shoot ratios varied strongly among species (Fig. 2).

3.3. Soil and foliar nutrients

Soils were moderately acidic (5.7 ± 0.1) with high percent organic matter ($14.4\% \pm 1.5$) and relatively low P (23.1 mg kg^{-1} ± 3.0) (Appendix A). The only soil nutrient that

Fig. 2. Below-ground (black) and above-ground biomass (gray) for the five species tested in each habitat (Pa = Pasture; S = Secondary; Pl = Plantation). Error bars show the means ± SE for the total biomass.

varied among habitat types was Ca ($F = 7.6$, df = 2, $p = 0.0228$), which was higher in plantations and secondary forests than in pastures (Appendix A).

Foliar nutrient concentrations varied among habitats (Table 3) and by species. Foliar nutrient content often differed substantially between plantations and both other habitats: foliar N, P, Cu, and S were all significantly higher and Al was significantly lower in plantations compared to both secondary forests and pastures ($F > 16.0$, $p < 0.0001$ in all cases; Table 3).

Foliar but not soil nutrients appear to be related to seedling growth in several cases. Seedling height was significantly positively correlated with foliar N ($r = 0.35$, $p = 0.0060$) whereas biomass was marginally positively correlated with foliar N ($r = 0.27$, $p = 0.0406$). Both seedling height and total biomass were correlated with foliar Mg ($r = 0.31$, $p = 0.0050$), S ($r = 0.52$, $p < 0.0001$), and Cu ($r = 0.40$, $p = 0.0033$).

3.4. Costs and logistics

Based on our calculations, the cost of direct seeding in abandoned pastures is ~2–4 times higher compared to seeding under plantations and secondary forests depending on the level of maintenance given (Table 4). Planting seeds under pasture grasses requires substantially more site preparation and post-planting maintenance than in habitats where grass cover has been reduced. The estimated costs for planting nursery-raised tree seedlings at the same sites (Zahawi and Holl, 2009) were ~10 times higher per 100 seedlings before maintenance costs were taken into account and ~10–30 times higher after maintenance costs, which vary depending on the objectives of the planting effort and the initial vegetation type.

4. Discussion

4.1. General overview

Our results support several previous studies showing that late-successional, large-seeded trees can be successfully introduced into early stages of succession (Camargo et al., 2002; Hooper et al., 2002). We found surprisingly consistent trends among the five species tested and our results lead to several general conclusions regarding the efficiency of direct seeding under different restoration approaches. First, we found that although germination under recently abandoned pastures, young secondary forests, and tree plantations was similar, seedling survival was significantly higher under the tree plantations. Second, seedlings grew more quickly and had lower root:shoot ratios in plantations suggesting that the higher nutrient availability in that treatment enhanced growth. Third, the costs for direct seeding were considerably lower compared to planting nursery-raised seedlings at the same sites, although there are important trade-offs to the two approaches.
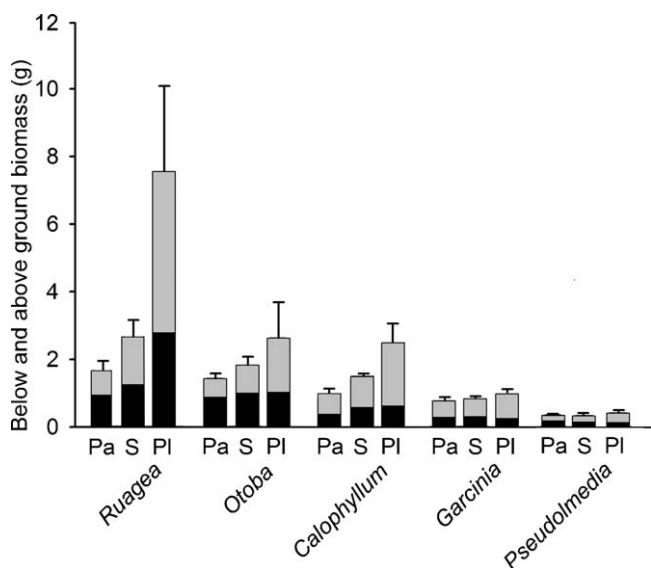
Table 4
Cost estimate (US$) to establish directly seeded tree species under plantations and secondary forests and in abandoned pasture. Comparative values for planting nursery-raised seedlings in abandoned pastures are also listed. Costs are per 100 individual seedlings surviving at 2 years following planting.

Habitat type	Direct seeding		Seedlings[a]
	Plantation and secondary forest	Pasture	Pasture
Task			
Locating and collecting seeds/ transfer seedlings to work site	$1–3	$1–3	$1.50–2
Nursery cost	–	–	$15–25
Transport expense (fuel 0–10 km)	$0.05	0.05	$0.25
Planting in the field	$2.50–3.50	$2.50–3.50	$20–25
Fertilizer/insecticide application	–	–	$0–10
Post-planting field maintenance	$1–2	$6–12	$80–120
Total estimate	$4.55–8.55	$9.55–18.55	$116.75–182.25

[a] The costs for the nursery-raised seedlings from estimates by Zahawi and Holl (2009).

Finally, there appear to be considerable advantages to using direct seeding as a complimentary measure to the more intensive restoration approach of planting fast-growing, N-fixing trees.

4.2. Habitat effects

In contrast to earlier tropical seed addition studies (Bonilla-Moheno and Holl, 2009; Camargo et al., 2002; Parrotta et al., 1997) we found that seed germination was relatively uniform among different habitat types (~43%). It is likely that burying seeds tended to equalize initial conditions among the habitats. Burial has been shown to improve germination rates of tree seeds in abandoned pastures (Cole, 2009; Doust et al., 2006) and reduce the incidence of seed predation (Garcia-Orth and Martinez-Ramos, 2008; Woods and Elliott, 2004).

Seedling survival and growth were consistently higher in the plantations than in either the secondary forests or the abandoned pastures. Surprisingly, there was no advantage for seedling survival in the 8–10-year-old secondary forests compared to pasture despite differences in overstory cover and amount of bare ground. However, light conditions in the understory of all three habitats may actually have been similar because our seedlings did not overtop the pasture grasses during the course of the study. Holl (1999) reported comparable light levels at soil surface under pasture grasses as in primary forest, and Hooper et al. (2002) found similar light levels under *Saccharum spontaneum* pasture grasses as under 95% shade cloth. Below-ground competition from pasture grasses in particular (e.g. Holl, 1999; Hooper et al., 2002; Nepstad, 1989), but also from ruderal herbs, shrubs, and lianas common to successional forests (Chen et al., 2008; Holl, 1998; Zahawi and Augspurger, 1999) have been shown to negatively affect seedling performance. So, it is also likely that seedlings in both the pastures and secondary forests experienced more below-ground competition than in plantations where the cover of grasses and ruderal herbs has been reduced.

Paralleling the results of seedling survival were marked differences in growth and allocation of above- and below-ground biomass among habitats. Seedlings in the plantations grew an average of 22–31% taller than those in either secondary forest or pasture. Interestingly, total biomass of the seedlings differed among all treatments (plantations > secondary forests > pastures). The root:shoot ratios mirrored this trend with pasture seedlings highest and seedlings in the plantations the lowest. Allocation of biomass to roots vs. shoots has long been thought to be an indicator of nutrient availability (Aikio et al., 2009; Bloom et al., 1985; Tilman, 1988). Several recent tropical studies suggest that nutrient limitations strongly affect seedling performance even in low light conditions. Palow and Oberbauer (2009) found that *Inga* seedlings allocated more biomass to roots and less to photosynthetic tissue when grown under shade on low-nutrient soil. Similarly, trenching increased biomass allocation to leaves vs. roots and significantly

increased N and P uptake in seedlings of two tropical tree species planted into treefall gaps and forest understory (Lewis and Tanner, 2000). Differences in nutrient availability between habitats may best explain the trends in survival and growth as suggested by the results the foliar nutrient analyses.

4.3. Foliar and soil nutrients

Seedlings in the plantations had higher foliar P, N, S, Mn, and Cu than those in either the secondary forests or plantations. Nitrogen can be limiting in tropical ecosystems (LeBauer and Tresender, 2008) and tropical reforestation studies indicate that foliar N is a good predictor of seedlings growth (Craven et al., 2007). Measurements on the later-successional trees used to establish the experimental plantations in this study show that foliar N was related to growth of the later-successional species (*Terminalia* and *Vochysia*) (Holl et al., 2010). Leaf litter measurements at three of the four sites used here also showed that total N content was highest in plantations, intermediate in secondary forests, and lowest in pastures (Celentano et al., 2010). The increased level of N in the plantations is most likely due to the planted *Inga* and *Erythrina* trees. Previous studies show that N-fixing trees, and *Inga* in particular, have enhanced seedling growth beneath their canopies (Carpenter et al., 2004b; Nichols et al., 2001).

4.4. Species effects

As with previous studies (Bonilla-Moheno and Holl, 2009; Camargo et al., 2002; Engel and Parrotta, 2001; Hooper et al., 2002; Sautu et al., 2006) we found considerable differences in germination among species ranging from 90% for *Garcinia* to only 25% for *Calophyllum*. The low germination of *Calophyllum* may have been due poor seed quality where large accumulations of fruit on the ground under parent trees increased the incidence of insect damage (Cole, personal observation). Although overall trends for survival were similar among habitats there were large differences in the performance of individual species. *Calophyllum*, *Otoba*, and *Ruagea* had relatively high mortality in pastures and secondary forests between year 1 and year 2 but performed well in plantations. In contrast, *Garcinia* had consistently high survival (≥70%) in all habitats and seems well suited to direct seeding in a range of conditions. Our results point up the importance of testing local trees in order to identify species that can be successfully seeded into the different types of habitat targeted for restoration.

4.5. Cost and logistics comparison

Clearly, there are important differences in the objectives of the two planting approaches that determine where/when planting seedlings vs. direct seeding will be most ecologically and economically effective. The results of the cost comparison show that direct

seeding is considerably less expensive and labor intensive (10–30-fold difference) than planting nursery-raised seedlings. This and other studies have shown that large-seeded and late-successional species can establish under pasture grasses and successional forests (Bonilla-Moheno and Holl, 2009; Cabin et al., 2002; Camargo et al., 2002; Doust et al., 2006; Hooper et al., 2002) but performance among individual species varies greatly and growth is often slow. Many species, including early-successional and small-seeded trees, will have higher establishment and growth rates when planted as seedlings (see Engel and Parrotta, 2001). Moreover, planting faster-growing, early-successional species will serve to more quickly change initial environmental conditions, shade out pasture grasses, and enhance establishment of later-successional species (Ashton et al., 2001; Holl et al., 2003; Lamb et al., 2005).

5. Conclusions

Direct seeding is a viable, low-cost approach for including late-successional species that do not colonize naturally into early stages of forest recovery. Seeding resulted in reasonable levels of seedling establishment (25–82% of germinated seeds) in pastures and young secondary forests and high levels of establishment under plantations (62–89%). Because of the great variability in species performance, testing and selection of local trees suitable for planting in targeted habitats prior to major direct seeding efforts will improve the efficiency of restoration projects. The extent of restoration possible through this method will be largely determined by the availability of local seed sources and sufficient quantities of viable seeds. When the restoration objectives are to rapidly establish canopy cover or restore large areas, then planting fast-growing nursery-raised seedlings is a more effective but higher cost approach. Our experience suggests that introducing late-successional seeds under restoration plantings, particularly when there are N-fixing trees, can yield high numbers of established seedlings and rapid growth. We therefore recommend direct seeding as a complimentary step to more intensive restoration efforts.

Acknowledgements

Appendix A.

Soil variable	Pasture	Secondary	Plantation
Bulk density (g cm^{-3})	0.8 ± 0.1^a	0.8 ± 0.6^a	0.7 ± 0.8^a
pH	5.8 ± 0.2^a	5.7 ± 0.2^a	5.6 ± 0.2^a
Organic matter (%)	13.6 ± 2.1^a	14.6 ± 3.2^a	15.1 ± 2.8^a
ENR	127.0 ± 1.1^a	126.8 ± 1.1^a	127.3 ± 1.1^a
Bray P (mg kg^{-1})	19.2 ± 3.9^a	21.5 ± 3.3^a	28.5 ± 7.7^a
K (mg kg^{-1})	148.8 ± 21.7^a	178.8 ± 38.1^a	119.5 ± 20.0^a
Ca (mg kg^{-1})	1058.3 ± 185.3^a	1397.3 ± 186.9^b	1377.3 ± 268.0^b
Mg (mg kg^{-1})	217.3 ± 36.9^a	257.0 ± 20.9^a	253.3 ± 35.5^a
Na (mg kg^{-1})	30.0 ± 4.2^a	31.3 ± 1.3^a	33.5 ± 1.6^a
Al (mg kg^{-1})	1680.1 ± 35.8^a	1550.8 ± 134.9^a	1638.0 ± 88.7^a
Fe (mg kg^{-1})	73.7 ± 12.8^a	100.5 ± 15.8^a	75.2 ± 13.1^a
Mn (mg kg^{-1})	34.8 ± 8.8^a	49.5 ± 17.8^a	56.8 ± 18.1^a
Cu (mg kg^{-1})	6.0 ± 0.3^a	5.5 ± 0.6^a	7.3 ± 0.7^a
Zn (mg kg^{-1})	2.6 ± 0.6^a	2.5 ± 0.9^a	3.2 ± 0.5^a

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