

RESEARCH ARTICLE

Direct Seeding to Restore Tropical Mature-Forest Species in Areas of Slash-and-Burn Agriculture

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Abstract

After tropical lands have been abandoned from anthropogenic pressures, often forest structure and some species recover naturally. Studies suggest, however, that mature-forest species are frequently slow to establish and an active management strategy may be necessary. We tested direct seeding of mature-forest species as a restoration strategy in sites previously used for slash-and-burn agriculture in semi-evergreen, seasonal forest in the Yucatan peninsula, Mexico, and evaluated when in the successional process this strategy had the highest success rate. We planted three mature-forest species (*Brosimum alicastrum*, *Enterolobium cyclocarpum*, and *Manilkara zapota*) in three forest ages: recently abandoned (<5 years), young successional forest (8–15 years), and reference forest (>50 years). Overall, an average of 5–41% of planted seeds germinated, and

3–35% were present through the seedling stage. Only *M. zapota* had higher germination in the reference forest than in the other forest ages, whereas the other two species had similar percentage germination in all successional stages. Of the seeds that germinated in the 8–15 years sites and the reference forest, 58–95% of the seedlings survived through the end of the study, whereas survival in recently abandoned sites was less than 50% in most cases. Seedling height was generally similar across forest age categories. Our results suggest that direct seeding these mature-forest species after the first few years of natural succession could be a successful strategy to accelerate and guarantee their establishment.

Key words: enrichment planting, forest succession, shifting agriculture, tropical dry forest, Yucatan peninsula.

Introduction

As an increasing area of agricultural land is projected to be abandoned in the tropics (Wright & Muller-Landau 2006), it is necessary to develop strategies that facilitate its recovery. Many past studies have focused on identifying barriers that may prevent the recovery of woody vegetation after the abandonment of pastures, slash-and-burn agriculture, or logging sites (e.g., Guariguata & Pinard 1998; Holl et al. 2000; Zimmerman et al. 2000; Holl 2002). Some studies have shown that simply allowing sites to recover naturally without further manipulation may be enough to recuperate forest structure and some forest species (Brown & Lugo 1990; Aide et al. 2000; Finegan & Delgado 2000), although rates of recovery vary greatly (Holl 2007). Lack of seed dispersal, however, is among the principal recruitment barriers for tropical trees, in particular for large-seeded or mature-forest species (Guariguata & Pinard 1998; Miller 1999; Holl et al. 2000; Zimmerman et al. 2000),

and species composition in secondary and old forests may differ greatly (Aide et al. 2000; Hooper et al. 2002; Martínez-Garza & Howe 2003; Lamb et al. 2005).

Systems such as intensive monocultures or pastures may prevent the establishment of forest trees because they contain vegetation (e.g., grasses or early successional species), which have proven to be a major barrier for tree establishment (Holl 1998; Hooper et al. 2002; Ferguson et al. 2003; Hooper et al. 2005; Sampaio et al. 2007). Compared to those land uses, slash-and-burn systems generally recover more rapidly (Fox et al. 2000; Ferguson et al. 2003; Finegan & Nasi 2004), but it is unclear the extent and the rate at which mature-forest or “deep-forest” species (as they are referred by Martínez-Garza & Howe 2003) are able to establish once sites have been abandoned.

If mature-forest species do not colonize during the first few decades of forest succession after land abandonment, not only are they at risk of extinction (Martínez-Garza & Howe 2003), but this may also jeopardize some forest functions and the presence of organisms that rely upon them (Chapman & Onderdonk 1998; Laurance 2006). In these cases, planting seeds or seedlings of these target species may be necessary to ensure their presence and accelerate the forest recovery process (Aide & Cavelier 1994; Zimmerman et al. 2000; Cabin et al. 2002; Martínez-Garza & Howe 2003; Martínez-Garza et al. 2005).

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Testing direct seeding into different forest stages is an important strategy to determine when during the successional process the introduction of these species results in the most successful establishment. For example, will seeds germinate and survive immediately after land has been abandoned, or is it necessary to wait until a canopy cover and/or appropriate soil conditions have established before introducing them? Because resources for restoration are limited, these experimental studies can help develop useful management recommendations (Chazdon 2003).

We direct seeded three mature-forest species into forests of three successional categories following slash-and-burn agriculture on the Yucatan peninsula in Mexico to evaluate (1) whether direct seeding is an effective strategy to establish later-successional species in shifting agricultural systems; and (2) the effect of fallow time on germination and establishment of native tree species.

Methods

This study was conducted in the Otoch Ma'ax Yetel Kooch (OMYK) reserve, located at the border of Yucatan and Quintana Roo states in the center of the Yucatan peninsula, Mexico (20°38' N, 87°37' W) [CONANP (Comisión Nacional de Áreas Naturales Protegidas) 2006]. Like much of the tropics, the Yucatan peninsula is a mosaic of land under different successional stages due to human practices, as well as natural events, such as hurricanes and fires, which have promoted a continuous cycle of forest disturbance followed by recovery for centuries (Challenger 1998; Allen et al. 2003). For centuries, the main productive activity in this area has been slash-and-burn agriculture (Anderson et al. 2004), in which plots are farmed for 1–2 years and then abandoned to natural regeneration. Milpas are rotational systems, which generate a continuous cycle of disturbance followed by forest recovery. This practice has created a landscape of successional vegetation ranging from sites that are currently in use to sites where abandonment age varies from less than 1 year to forest older than 50 years. Maize is the primary crop planted, but squash, beans, and some seasonal fruits can be planted. The dominant natural vegetation (approximately 93% of total cover) is semi-evergreen seasonal forest (selva mediana subperennifolia, Pennington & Sarukhán 2005).

Mean annual precipitation (1941–2005) for Quintana Roo State (QR) was 1,263 mm, and for Yucatan State (YT) was 1,091 mm with the vast majority of the precipitation falling between June and October. Precipitation in 2005 was slightly above average due to high hurricane activity in the region (QR: 1,456.4 mm; YT: 1,107.5 mm), whereas in 2006 it was below average (QR: 1,131.3 mm; YT: 891.2 mm) [CONAGUA (Comisión Nacional del Agua) 2005, 2006].

Soils are generally very shallow (<10 cm in depth) and underlain by limestone. The two most abundant soil types in the reserve are rendzinas on limestone, and lithosols (CONANP 2006), that according to Mayan nomenclature correspond to *ek'ulum* (dark humus layer) or *kancab* (reddish humus layer). Soils were neutral (pH 6.9 ± 0.03 SE)

with higher organic matter in reference forest ($26.3 \pm 1.8\%$) than recently abandoned ($20.0 \pm 1.3\%$) or young successional ($21.6 \pm 1.0\%$) sites (Bonilla Moheno 2008).

Sites

We direct seeded three later-successional tree species and measured seed germination, seedling survival, and seedling growth in nine sites, three replicates of three forest age categories: recently abandoned slash-and-burn plots (*milpas*) (<5 years), young secondary forest (approximately 8–15 years), and reference forest (>50 years). Distance between sites in the same age category ranged from 1 to 3 km, and recently abandoned and young secondary forest sites range from 500 m to 1 km from reference forest patches (>50 years). Sites recently abandoned and young successional forests were approximately 3 ha in size. Patches of reference forest were greater than 5 ha.

A vegetation survey of 45 sites in the area (including the secondary forest sites, and reference forest sites used in this study) showed that vegetation structure and species composition varies greatly across forest age categories (Bonilla Moheno 2008). The canopy height ranges from 1.5 to 3.0 m in recently abandoned plots to 10–15 m in secondary forest and 25–30 m in reference forest. Recently abandoned sites have high herbaceous vegetation cover and stems of some secondary forest species, largely due to resprouting, but do not have a closed canopy. Young secondary forest sites have low herbaceous vegetation cover and higher stem density than either younger than 5 years or older than 50 years sites. The number of species increases over time with the highest values in reference forest. The dominant species in secondary forest include *Bursera simaruba*, *Lisyloma latisiliquum*, and *Caesalpinia gaumeri*, whereas *Brosimum alicastrum*, *Malmea depressa*, and *Manilkara zapota* are common in the reference forest (see Bonilla Moheno 2008 for more detailed vegetation composition).

Species

The three later-successional tree species used for the experiment were *B. alicastrum* Sw. (Moraceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae Mimosoidae), and *M. zapota* (L.) Royen (Sapotaceae). Cohorts of *B. alicastrum* and *E. cyclocarpum* were sowed in both 2005 and 2006; *M. zapota* was planted only in 2006. In general, these species fruit during the first half of the rainy season (April–September) in this region (Vázquez-Yañes et al. 1999).

All these species are shade-tolerant (Vázquez-Yañes et al. 1999) and are found primarily in the reference forest (Bonilla Moheno 2008). All species have fleshy fruits and large seeds (*E. cyclocarpum* approximately 2.3×1.5 cm, *B. alicastrum* approximately 1.0×1.8 cm, *M. zapota* approximately 2.0×1.0 cm) that are dispersed mostly by birds and bats (Vázquez-Yañes et al. 1999). These three species are among the most important tree species in the diet of spider monkey (fruits of *B. alicastrum* and *M. zapota*, and young leaves of *E. cyclocarpum*, Ramos-Fernández 2008, CIIDIR, Oaxaca, personal

communication), which is one of the main reasons the OMYK area was protected (Ramos-Fernández & Ayala-Orozco 2003). These species, however, are rarely found to be regenerating in secondary forests (Bonilla Moheno 2008). In addition, *B. alicastrum* and *M. zapota* have been identified by the National Commission for the Knowledge and Use of Biodiversity as potentially valuable species for restoration purposes (Vázquez-Yañes et al. 1999).

Planting Experiments

The National Commission of Forestry (CONAFOR), region XII Yucatan, provided all seeds, which were collected from regional trees and stored in refrigerators. We tested seed for viability using flotation tests and only used viable seeds. Viable seeds of *E. cyclocarpum* were scarified by immersing them in boiling water for 1 minute (Vázquez-Yañes et al. 1999). In addition, all seeds were left overnight in water to imbibe prior to planting.

We planted 1,800 seeds per species: 200 seeds of each species in each of three replicates (sites) per forest age. Within each site, we established four blocks that were randomly located and separated by at least 50 m. Within each block, we established 2 × 1 m plots for each species that were separated by at least 1 m. In each plot, we placed 50 seeds in a 5 × 10 seed grid with seeds separated by 20 cm. Planting was done by removing the litter layer and burying seeds in the mineral soil (approximately 3- to 5-cm deep) during the rainy season (June–December), as seed burial has been shown to increase germination and establishment (Woods & Elliott 2004; Doust et al. 2006; Garcia-Orth & Martínez-Ramos 2007). After seeds were sowed, no management was performed around the plots or seedlings because we wanted to evaluate seed and seedling performance under natural conditions.

We measured germination, survival, and growth for 2 years for the 2005 cohort (planted in September), and for 1 year for the 2006 cohort (planted in June). Germination was recorded when the radicle emerged. Seedlings were censused for survival and growth 1 month after the planting and every 2–3 months thereafter. Final height of the apical meristem was measured to the nearest centimeter.

Data Analyses

Measurements from the four plots in the same site were combined prior to all statistical analyses except correlations. Percent germination and seedling establishment were ranked to meet assumptions of normality and homogeneity of variance; the untransformed data are reported (mean ± 1 SE), however, for clarity of interpretation. Height data were square-root transformed. Seed germination is the maximum number of seedlings present at any point of the study/total seeds (200); seedling survival is the number of seedlings present at a given census period/number of seeds that germinated; seedling establishment is defined as the number of seedlings alive at the last census/total seeds planted.

We used two-way analysis of variance (ANOVA) for *E. cyclocarpum* and *B. alicastrum*, and one-way ANOVA for *M. zapota*, to analyze the effect of year and forest age category on seed germination. We used one-way ANOVA to evaluate the effect of forest age category on seedling establishment and final height for each species for each cohort (2005, 2006) separately, as survival and growth of the two cohorts was measured for different time periods. We compared seedling survival of each species across forest categories using survival analyses. We tested for differences in survival times among forest categories using the log-rank chi-square test (χ^2) of homogeneity between groups of the Kaplan-Meier product-limit survival analyses using JMP 7.0.1. We calculated the Spearman's correlation coefficient (r) between number of seedlings and final average height (at the plot level) to evaluate whether there were density-dependent effects on growth.

Results

Mean germination for all species across sites in 2005 and 2006 was 41.4 ± 7.2% and 41.3 ± 6.1%, respectively. The highest germination recorded was for *E. cyclocarpum* (2005) in the reference forest (41.2%), whereas the lowest germination was for *M. zapota* in recently abandoned sites in 2006 (5.2%; Table 1). For both *E. cyclocarpum* and *B. alicastrum*, percent seed germination did not differ significantly across forest age in either year (no significant forest age × year interaction,

Table 1. Percent seed germination (mean ± SE) for three species planted into three forest age categories in the Yucatan peninsula (2005 and 2006).

	Germination		
	<5 Years	8–15 Years	>50 Years
<i>Brosimum alicastrum</i>			
2005	13.7 ± 5.6	5.5 ± 0.5	7.7 ± 1.6
2006	10.8 ± 5.8	37.5 ± 20.4	34.8 ± 4.9
<i>Enterolobium cyclocarpum</i>			
2005	26.7 ± 9.2	29.2 ± 6.6	41.2 ± 2.9
2006	26.3 ± 5.4	17.2 ± 3.1	21.3 ± 5.8
<i>Manilkara zapota</i> (2006)	5.2 ± 2.1 (a)	10.7 ± 1.4 (a)	28.8 ± 3.8 (b)

$n = 3$ sites per forest age category (FA); 200 seeds planted at each site. Different letters indicate significant differences with Tukey-Kramer mean comparison across forest categories ($p < 0.05$). Two-way ANOVA—*B. alicastrum* (Year: $F_{1,12} = 7.3$, $p = 0.019$; FA: $F_{2,12} = 0.5$, $p = 0.589$; Year × FA: $F_{2,12} = 2.6$, $p = 0.114$), *E. cyclocarpum* (Year: $F_{1,12} = 4.9$, $p = 0.046$; FA: $F_{2,12} = 0.7$, $p = 0.498$; Year × FA: $F_{2,12} = 1.4$, $p = 0.288$), One-way ANOVA—*M. zapota* $F_{2,6} = 34.2$, $p < 0.001$.

Table 1). In contrast, *M. zapota* seeds germinated more in forests older than 50 years than in the other two forest ages. Seed germination was significantly higher for *E. cyclocarpum* in 2005 and for *B. alicastrum* in 2006 (Table 1).

Most seedlings died during the beginning of the dry season (February) for the 2005 cohort and at the end of the rainy season (November–December) for the 2006 cohort, with minimal mortality thereafter (Fig. 1). In general, seedlings showed lower survival in the recently abandoned milpas (<50% in most cases) compared to the early secondary forest and the reference forest, where 58–95% of seedlings survived (2005: *B. alicastrum*: $\chi^2 = 35.8$, $p < 0.001$; *E. cyclocarpum*:

$\chi^2 = 92.8$, $p < 0.001$; 2006: *B. alicastrum*: $\chi^2 = 66.6$, $p < 0.001$; *M. zapota*: $\chi^2 = 31.5$, $p < 0.001$). *Enterolobium cyclocarpum* (2006), however, had similar seedling survival across all forest ages, ranging from 65.9 to 74.2% ($\chi^2 = 0.03$, $p = 0.982$; Fig. 1).

Seedling establishment from introduced seeds ranged from 2.5 to 35.5% at the end of the study (Table 2). In most cases, older forest categories had higher seedling establishment than recently abandoned milpas, but this difference was only significant for *E. cyclocarpum* (2005) and *M. zapota*. *Enterolobium cyclocarpum* (2006) had similar numbers of seedlings across forest ages.

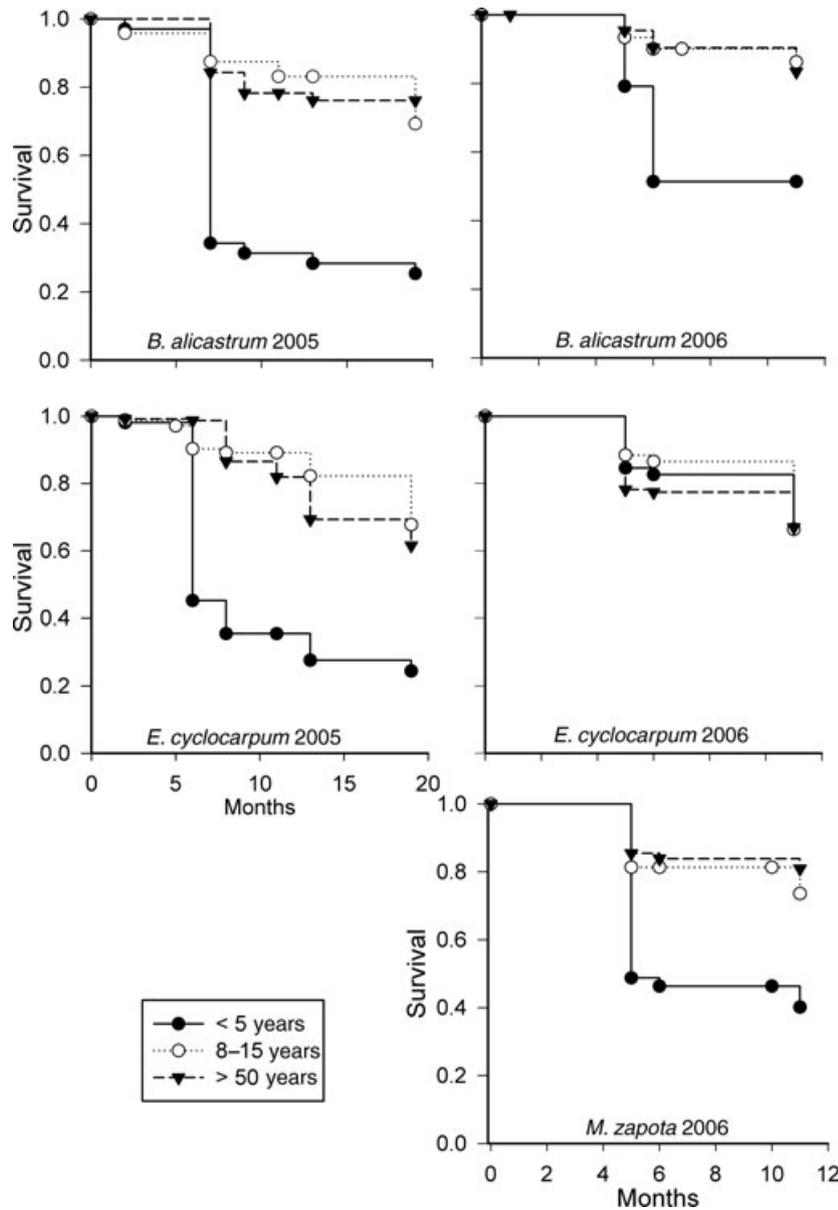


Figure 1. Survival estimates (Kaplan-Meier) of species by forest age category in the Yucatan peninsula. Mean survival time (months) for each category (<5, 8–15, and >50 years, respectively: 2005—*E. cyclocarpum*: 10, 17, 16; *B. alicastrum*: 10, 17, 12; 2006—*E. cyclocarpum*: 10, 10, 10; *B. alicastrum*: 6, 10, 10; *M. zapota*: 8, 10, 10). Seeds were planted in September 2005 and June 2006.

Table 2. Percent establishment from planted seeds (mean \pm SE) 1 (2006) and 2 (2005) years after planting for three species in three forest ages in the Yucatan peninsula.

	Final Seedling Establishment		
	<5 Years	8–15 Years	>50 Years
<i>Brosimum alicastrum</i>			
2005	3.0 \pm 2.7	3.3 \pm 1.6	7.3 \pm 1.6
2006	7.5 \pm 4.3	35.5 \pm 19.7	33.3 \pm 4.5
<i>Enterolobium cyclocarpum</i>			
2005	4.6 \pm 4.1 (a)	20.6 \pm 7.5 (ab)	25.8 \pm 2.1 (a)
2006	19.5 \pm 5.1	12.3 \pm 1.6	14.6 \pm 4.9
<i>Manilkara zapota</i> (2006)			
	2.5 \pm 2.2 (a)	10.3 \pm 1.8 (b)	25.2 \pm 4.4 (b)

$n = 3$ sites per forest age category; 200 seeds planted at each site. Different letters indicate significant differences with Tukey-Kramer mean comparison across forest categories ($p < 0.05$). One-way ANOVA $df = 2, 6$ in all cases. *B. alicastrum* (2005: $F = 1.0$, $p = 0.421$; 2006: $F = 1.6$, $p = 0.268$), *E. cyclocarpum* (2005: $F = 5.8$, $p = 0.038$; 2006: $F = 0.8$, $p = 0.489$), *M. zapota* ($F = 21.9$, $p < 0.001$).

At the final census, seedling height was similar across forest successional stage (2005: *B. alicastrum*: $F_{2,6} = 0.6$, $p = 0.581$; *E. cyclocarpum*: $F_{2,6} = 1.0$, $p = 0.418$; 2006: *B. alicastrum*: $F_{2,6} = 0.6$, $p = 0.562$; *E. cyclocarpum*: $F_{2,6} = 0.004$, $p = 0.995$; Fig. 2) with high variation within forest age categories. Only *M. zapota* had marginally shorter seedlings in the reference forest than in the other forest age categories ($F_{2,6} = 5.2$, $p = 0.048$). The final number of seedlings in 2005 was positively correlated with the final seedling height (per plot) (*B. alicastrum* $r = 0.32$, $p = 0.041$; *E. cyclocarpum* $r = 0.36$, $p = 0.011$). In 2006, however, these same species were not significantly correlated (*B. alicastrum* $r = 0.22$, $p = 0.268$; *E. cyclocarpum* $r = 0.18$, $p = 0.310$), and number of surviving seedlings of *M. zapota* were negatively correlated with their height ($r = -0.47$, $p < 0.001$).

Discussion

The success of direct seeding as a strategy to ensure the presence of mature-forest species in areas previously used for agricultural practices will depend on two factors: seed germination and seedling survival. In our study, percent germination ranged from 5 to 41% with no consistent trend across forest age. Past studies in recently abandoned pasture and agricultural lands elsewhere in the tropics show similar or lower germination with high variation among species (e.g., Ray & Brown 1995; Sun & Dickson 1996; Hardwick et al. 1997; Parrotta et al. 1997; Hooper et al. 2002; Woods & Elliott 2004; Doust et al. 2006; Garcia-Orth & Martínez-Ramos 2007; Sampaio et al. 2007). We know of no previous studies that have compared germination of later-successional species across a chronosequence of forest ages, but Holl (1999) did not find consistent differences in germination of several early successional species in recently abandoned pasture and reference forest. Aerts et al. (2006) found higher germination under shrub canopies than in the open in degraded savannas in Ethiopia.

We used seedling methodologies likely to be used by restoration practitioners. Several factors, however, could have affected the germination rates we recorded. We tried to

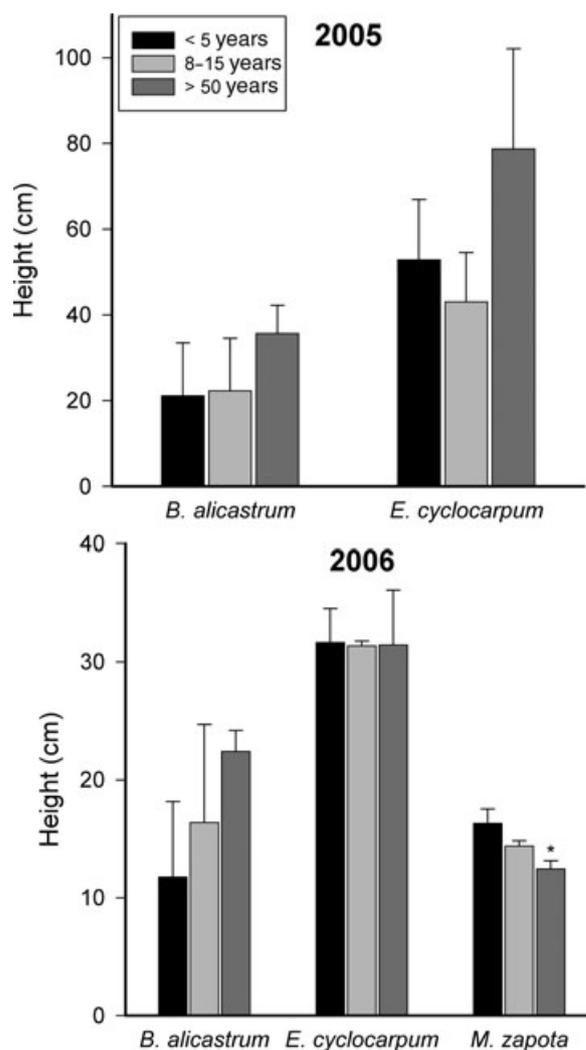


Figure 2. Seedling height by forest age category after 2 years (2005, top) and 1 year (2006, bottom) cohorts in the Yucatan peninsula. Values are mean \pm SE. Asterisk (*) indicates significant difference ($p < 0.05$) for *M. zapota* based on post hoc Bonferroni corrections. $n = 3$. Note different y-axis scales.

decrease the risk of using nonviable seeds by testing for viability and scarifying one species. It is possible that the source of seeds could have affected our results, as all our seeds were collected from regional but not local individuals. Seeds were stored in a refrigerator until planted which also might have affected germination. Finally, we did not measure seed predation, which can be high in abandoned agricultural lands (reviewed in Holl 2002).

Germination is highly seasonal in dry forests including the Yucatan peninsula (Lieberman & Li 1992; Ray & Brown 1995; Khurana & Singh 2001; Cabin et al. 2002; Ceccon et al. 2004), and the time of dispersal during the rainy season may affect seedling establishment (Blain & Kellman 1991; Doust et al. 2008; Vieira et al. 2008). Variation in time of planting (September 2005—middle of the rainy season vs. early June 2006 - beginning of rainy season) might be a cause for interannual differences in germination, although the two species showed higher germination in different years.

Once seeds germinated, their survival was high, 58–95% in young successional and reference forest, and lower than 50% survival in recently abandoned milpas. Previous studies also have shown higher survival from large-seeded species (Hooper et al. 2002; Doust et al. 2008). The fact that there were no differences in survival of those species introduced 8–15 years after milpas abandonment and those in sites older than 50 years, suggests basic environmental conditions are suitable for establishment within a decade. Herbaceous and shrubby vegetation colonize quickly in milpas (Bonilla Moheno 2008) and many past studies have shown that early successional vegetation competes with later-successional trees (reviewed in Holl 2002). Moreover, past studies indicate that high light and temperature conditions in recently abandoned sites often result in reduced seedling survival, particularly of later-successional species (Pinard et al. 1994; Ray & Brown 1995; Hardwick et al. 1997; Loik & Holl 1999; Cabin et al. 2002; Vieira & Scariot 2006; but see Camargo et al. 2002). Therefore, waiting until the canopy develops and shades out these early successional species is recommended before introducing later-successional species.

Water availability has been suggested as the most important limiting factor for establishment and survival of dry forest trees (Lieberman & Li 1992; Ray & Brown 1995; Cabin et al. 2002). Although the timing of the rainy season was similar in both years, the intensity differed due to the impact of two hurricanes in 2005: one before seeding and the second 1 month after seeding. These resulted in temporal flooding of some sites, which might have killed some seeds and seedlings. Despite these differences, survival in young successional and reference forests was high for all species in both years. Percent survival of *E. cyclocarpum* in recently abandoned sites forest after 1 year was quite different, 11.5 and 74.2% for the 2005 and 2006 cohorts, respectively; however, it is impossible to determine a cause for this difference without further experimentation.

Despite differences in canopy height and composition across forest ages, height of planted seedlings was generally similar. This result is somewhat surprising given that most

past studies have shown that seedling survival is lower, but growth is higher in more open conditions, such as those in recently abandoned sites (Ray & Brown 1995; Ceccon et al. 2004; Vieira et al. 2007). One possible explanation is that percent canopy cover in dry forests, such as the one studied, varies substantially during the year with much higher light in the understory during the dry than in the wet season (Cervantes et al. 2005; Kalacska et al. 2005; Vieira & Scariot 2006). Moreover, some later-successional species may be photoinhibited in high light conditions (Loik & Holl 2001). Intraspecific competition among seedlings did not seem to explain the lack of differences in growth, as final seedling height and seedling establishment were positively correlated for the largest seedlings (*E. cyclocarpum* from 2005). We only recorded height rather than above and belowground biomass, and it is likely that our seedlings allocated substantial resource to root growth (Montgomery & Chazdon 2002). *Enterolobium cyclocarpum*, an N-fixer, increased in height more than the other species, which is consistent with results from Wishnie et al. (2007) who recorded high growth of this species in former pasture land in Panama.

Direct seeding of mature-forest species has been suggested as a more feasible small-scale restoration strategy in terms of financial and time investment than planting seedlings, as seedlings are much more costly to produce and require nursery facilities (Engel & Parrotta 2001; Hooper et al. 2002; Finegan & Nasi 2004; Sampaio et al. 2007). Moreover, using seeds does not damage roots of resprouting species (Sampaio et al. 2007), which is an important mode of regeneration in many tropical dry forests (Miller & Kauffman 1998; Kennard 2002). For rare species or species that fruit infrequently, however, seeds sources may be limiting making propagating seedlings in a nursery a more favorable approach. Several authors suggest that introducing trees as seedlings, or as mixture of seedlings and seeds might be a more successful strategy to overcome limited germination and seed sources, but will require more resources at the outset (e.g., Ray & Brown 1995; Hardwick et al. 1997; Engel & Parrotta 2001; Camargo et al. 2002). Therefore, a number of factors will have to be weighed to determine how to most efficiently introduce different species of plants at given sites. Direct seeding seems to be particularly well suited for introducing later-successional species once the forest canopy has closed, when it would be difficult to plant seedlings without damaging stems of naturally recruiting species.

Implications for Practice

- Some tropical forest trees that are slow to colonize naturally can be introduced successfully by sowing their seeds into abandoned slash-and-burn sites.
- Given that seed germination is often less than 50% and variable, it will be necessary to introduce more propagules than planting seedlings. Therefore, germination rates, abundance of seed sources, availability of seedling propagation facilities, costs, and damage to

resprouts from planting will need to be weighed for specific sites and species to determine the most appropriate introduction method.

- Seeds or seedlings of later-successional species should be introduced into milpas once a canopy has established (e.g., 8–15 years after abandonment) rather than immediately following abandonment to maximize seedling survival.

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