

Effects of Selective Vegetation Thinning on Seed Removal in Secondary Forest Succession¹

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ABSTRACT

Seed removal was assessed for two tree species in three forest types: (1) secondary forest with and (2) without selective vegetation thinning, and (3) mature forest. Selective vegetation thinning meant the removal of all stems ≤ 3 cm in diameter of secondary-forest species and was intended as a management technique to accelerate succession toward mature forest. Thinning did not have an effect on seed removal. One of the species showed lower seed removal in mature forest compared to secondary forest.

RESUMEN

Se midió la remoción de semillas de dos especies de árboles en tres tipos de bosque: (1) bosque secundario con y (2) sin aclareo selectivo de vegetación, y (3) bosque maduro. El aclareo selectivo de vegetación consistió en la remoción de todos los tallos ≤ 3 cm de diámetro de especies de bosque secundario, y se aplicó con la finalidad de acelerar la sucesión hacia bosque maduro. El aclareo no tuvo efecto sobre la remoción de semillas. La remoción de semillas de una de las especies fue menor en bosque maduro que en bosque secundario.

Key words: forest management; Mexico; secondary forest; seed removal; succession; tropical dry forest; vegetation thinning.

PRIMARY TROPICAL FORESTS (*I.E.*, MATURE UNDISTURBED FOREST) IN THE WORLD are disappearing at an alarming rate. Often, after clearing primary forest for agriculture and subsequent abandonment, secondary forest develops (Brown & Lugo 1990, Guariguata & Ostertag 2002). The uses and ecological services of secondary forests are potentially many, although generally overlooked (Finegan 1992, Mizrahi *et al.* 1997). This type of vegetation is likely to increase in area over time, both due to continued clearing of primary forest as well as abandonment of agricultural areas. However, applied research focusing on management techniques for these forests is still relatively scarce (Guariguata 1999).

One group of management techniques that has been applied in secondary forests is the one that involves vegetation removal. For example, “liberation thinning” implemented in Costa Rica consisted of the elimination of competitor trees around target crop trees in order to enhance the growth of the latter (Hutchinson 1993, Guariguata 1999). In an ongoing research in the Yucatan Peninsula, “acahual thinning” involves the removal of all stems < 2 cm in diameter in secondary forest (locally named “acahual”) and is being applied as a restoration technique in order to reduce stem density and thus achieve architectural characteristics similar to those in mature forest (Allen *et al.* 2003). It is expected that

such management will help break the fire cycle that apparently maintains the vegetation in a stage of arrested succession. It is also believed that if removal of stems in secondary forests is done selectively, such that only plant species of secondary vegetation are cut, the survival/growth of mature forest saplings/trees may be favored. This could potentially achieve not only architectural characteristics, but also a species composition more similar to mature forest, and may potentially accelerate succession toward mature forest (Pérez-Salicrup & Allen, pers. obs.). We call such a treatment as “selective vegetation thinning.”

Selective vegetation thinning could have other ecological effects, besides the intended management goals. Consequently, we need to not only assess the success of this practice in favoring survival and growth of mature-forest tree species, but also its effect on other ecological processes involved in forest regeneration and succession. For example, selective vegetation thinning could affect various aspects of seed dynamics, which are known to be very important both in natural regeneration and succession, as well as in restoration management of forest systems (Chambers & MacMahon 1994, Bakker *et al.* 1996, Guariguata & Pinar 1998, Khurana & Singh 2001).

One important aspect of seed dynamics that greatly affects plant demography is post-dispersal seed removal (Hulme 1997, 1998; Crawley 2000). In Neotropical forests, rodents are the most important seed harvesters of medium–large seeds (> 3 mm; Hulme 1998, Forget *et al.*

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2002). The abundance and activity of rodents depend, among other factors, on structural habitat characteristics. For example, the abundance of small rodents, and also rodent seed predation, tend to be lower in areas with lower vegetation density (Hulme 1998 and references therein). Moreover, previous studies have suggested that lower levels of seed predation by rodents are found in areas with increased litter cover (e.g., Hammond 1995). As vegetation thinning alters the structure of the vegetation in the area where it is applied, creating a more open habitat and with greater amount of woody debris on the forest floor, it may also affect the rates of seed removal. The objective of this study was to assess whether seed removal rates differ in three forest types: secondary forest with selective vegetation thinning, unthinned secondary forest, and mature forest. In particular, we predicted that seed removal by rodents may be decreased in areas where selective vegetation thinning is applied.

Field work was conducted in a seasonally dry forest in the northern Yucatan Peninsula of Mexico, where most of the vegetation is the result of a long history of disturbances by humans, fire, tree harvesting, and hurricanes, and where secondary vegetation dominates the landscape (Olmsted *et al.* 1995, Allen *et al.* 2003). The experiment took place at Reserva Ecológica “El Edén” (1492 ha), located 38 km northwest of the city of Cancún, in the state of Quintana Roo. Mean annual temperature and precipitation in the region are 24.7°C and 1511 mm, respectively, with most of the rainfall occurring between June and December (Pedroza-Espino 2003).

Secondary forest at the study site is characterized by very dense vegetation formed by trees that resprout after recurrent fires. However, although resprouting is abundant, secondary forests at “El Edén” appear to be in a stage or arrested succession, with a very slow progression toward mature forest. Mature forest, on the other hand, is characterized by an open understory due to a decrease in stem density and an increase in the diameter of trees (Allen *et al.* 2003).

In October 2001, ten 30 × 30 m secondary-forest plots were established to conduct an experiment to assess the effect of selective vegetation thinning on growth and survival of mature-forest trees (Pérez-Salicrup & Allen, pers. obs.). Secondary-forest sites where these plots were established varied between 5 and 25 yr of successional age, following clearing and burning of vegetation. Thus, these plots were placed in pairs: one pair in each site, with at least 30 m between plots in a pair, and at least 200 m between sites. One member of each pair was randomly chosen for selective vegetation thinning. The thinning treatment consisted of cutting with a machete all saplings ≤ 3 cm in diameter at 1.3 m (DBH) of tree species characteristic of early successional stages, as well all but the largest stem in all multiple-stemmed trees. The number of stems removed in the secondary-forest plots varied between 5700 and 17,000 stems/ha, which accounted for a total basal area of 0.6–4 m²/ha removed, or 6–18 percent of the original basal area. Thinning was also conducted in a 10-m wide buffer zone around thinned plots.

Seed removal was assessed in these ten plots and additionally in five mature-forest plots with the same dimensions between May and July 2002. The seeds of two tree species were used: *Bursera simaruba* (Burseraceae) and *Manilkara zapota* (Sapotaceae). These species were chosen because they are very abundant in the landscape of the Yucatán Peninsula. However, while *B. simaruba* is common in both mature and secondary forest, *M. zapota* is more common in mature forest. Seeds of *B. simaruba* are known to be eaten by rodents (Hammond 1995), and

although no data on seed predation exist for *M. zapota*, other species in this genus are known to be consumed by rodents (e.g., Forget *et al.* 2001). Also, the seeds of both species are of a size (approx. 5–10 mm long) that facilitated seed fate monitoring, and both are dispersed by frugivorous birds and mammals that defecate or regurgitate seeds (Klimstra & Dooley 1990, Graham *et al.* 2002). Finally, both species have overlapping fruiting seasons, which allowed for simultaneous setup of the experiment, thus avoiding confounding factors of temporal nature.

Twelve seed-removal stations (six for *B. simaruba* and six for *M. zapota*) were set out in each of the 15 plots. Each seed station consisted of three seeds placed directly on the forest floor, and their position was marked with a small flag. In each plot, seed stations were placed along three parallel transects in a regular setup, such that each seed station was 10 m away from any other station, alternating both seed species. A total of 90 seeds (three seeds × six stations × five replicates) were set out for each species per habitat (mature forest, secondary forest with thinning, secondary forest control). The number of seeds remaining in each station was counted daily for 5 d, then once a week for 1 mo, and finally after two more weeks had elapsed. The total duration of the experiment was 7 weeks, at which point the experiment was terminated because all seeds, except four *B. simaruba* seeds in the mature forest, had been removed or preyed on by rodents.

Seed removal was analyzed using survival analysis (failure-time analysis), which is the most appropriate statistical method for analyzing these kinds of data (Fox 2001). Analyses were cast as Generalized Linear Models, using the statistical program GLIM (Francis *et al.* 1993). The secondary-forest plots were in pairs such that replicates could have been treated as blocks. However, the primary forest plots subsequently established for the seed-removal study were in a separate area of the Reserve, and thus the statistical analyses could not incorporate the blocking effect. For *M. zapota*, a survival model with constant hazard, no censoring, and exponential error structure was defined (Crawley 1993). For *B. simaruba*, a survival model with constant hazard, censored data (as a few seeds still remained alive at the end of the study), and Poisson error structure with log link was defined (Crawley 1993). For both species a nested model was used, with two factors: forest type (mature forest, thinned secondary forest, control secondary forest) and plots nested within forest type. The independent variable was the number of days of survival (with each datum calculated as an average based on the three seeds in each seed-removal station). When the factor forest type was found to have a significant effect on the independent variable, multiple posteriori pair-wise comparisons were performed following the sequential Dunn–Sidak technique (Sokal & Rohlf 1995), yielding a corrected *t*-test for each comparison.

Seed removal was very high for both species in all three forest types, with 100 percent of *M. zapota* seeds and 93 percent of *B. simaruba* seeds removed in 4 weeks (Fig. 1). Mean survival time for *M. zapota* seeds was 5.8 (SE = 1.16), 5.4 (SE = 1.37), and 4.6 (SE = 0.68) d in mature forest, thinned secondary forest, and control secondary forest, respectively. Survival analysis for this species detected no effect of plot ($\chi^2 = 17.43$, $df = 14$, $P > 0.1$) and also no differences of survival among the three forest types ($\chi^2 = 0.87$, $df = 2$, $P > 0.5$). Mean survival time for *B. simaruba* showed a similar trend as *M. zapota*, with 8.3 (SE = 2.85), 3.52 (SE = 0.86), and 2.53 (SE = 0.22) d in mature forest, thinned secondary forest, and control secondary forest, respectively. Survival analysis for this species did detect a significant effect of plot ($\chi^2 = 29.07$, $df = 12$,

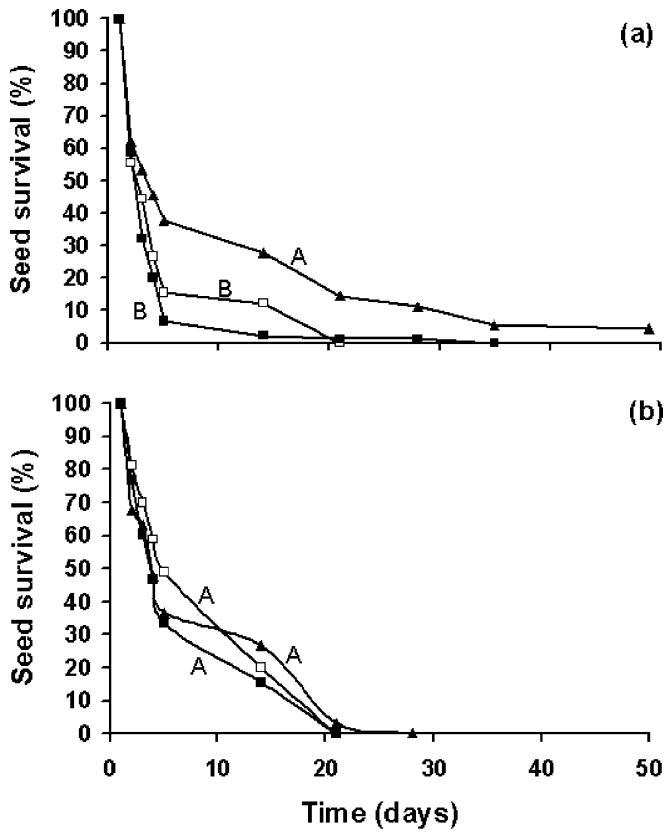


FIGURE 1. Survival over time for seeds of *Bursera simaruba* (a) and *Manilkara zapota* (b) in three habitats: secondary forest without selective vegetation thinning (filled squares), secondary forest with selective vegetation thinning (open squares), and primary forest (filled triangles). A total of 90 seeds for each species/habitat combination were used. Different letters next to lines indicate statistically significant differences in survival ($P < 0.05$).

$P < 0.005$) and a significant effect of forest type ($\chi^2 = 25.73$, $df = 2$, $P < 0.001$). A posteriori pair-wise comparisons showed that seeds in the primary forest suffered significantly lower removal than seeds placed in thinned secondary forest ($t = 3.52$, $df = 8$, $P = 0.0079$) and than seeds in control secondary forest ($t = 4.77$, $df = 8$, $P = 0.0014$), but no difference in removal was detected between thinned and control secondary-forest plots ($t = 1.28$, $df = 8$, $P = 0.24$).

Final seed fate was not assessed in this study, and while we assumed that seed removal equaled predation, some of the removed seeds might have survived if cached by scatterhoarding rodents. However, seeds of the sizes used in this experiment (5–10 mm) are believed to be generally eaten rather than scatterhoarded (Forget *et al.* 1998). Even if some of the removed seeds had initially been cached by rodents, available evidence suggests that their probability of long-term survival and seedling establishment would be very low (Hulme 2002 and references therein).

Regarding general aspects of post-dispersal seed predation in Neotropical forests, the results of this research coincide with those of several recent studies, and at least three general trends can be confirmed. First, seed predation can be very high and consequently represent a lim-

iting factor for forest regeneration and succession in secondary forests (*e.g.*, Hammond 1995, Notman & Gorchoy 2001, Peña-Claros & de Boo 2002). Second, seed predation is often (although not always, see Holl & Lulow 1997) lower in mature forest when compared to successional forest stages (*e.g.*, Hammond 1995, Peña-Claros & de Boo 2002) or otherwise disturbed forest (*e.g.*, logged forest fragments, Guariguata *et al.* 2002). The mature forest at our study site is characterized by higher tree diversity as well as lower tree density and larger tree size, compared to secondary forest (Schultz 2003). Our results suggest that seed predators may be partly responsible for slowing the establishment in secondary forest of some tree species that are common in mature forest (Allen *et al.* 2003). Finally, much variation exists in seed predation dynamics, and it is generally species and site specific (Holl & Lulow 1997, Forget *et al.* 2001, Notman & Gorchoy 2001, Guariguata *et al.* 2002, Peña-Claros & de Boo 2002).

In terms of the effects of selective vegetation thinning on seed removal, we found that this management technique had no effect on the seed removal rates of the two tree species tested. It was hypothesized that selective vegetation thinning, by decreasing vegetation density and increasing woody debris on the forest floor, could cause a decline both in rodent populations and in their ability to detect seeds, thus decreasing seed removal rates and favoring tree regeneration. However, it is known that the population of rodent seed predators can vary greatly in space and time and that their overall effect on seed fate is contingent upon other factors not accounted for in this study (*e.g.*, Notman & Gorchoy 2001, Feer & Forget 2002). Additionally, other animal groups (*e.g.*, ants, bruchids) can be important post-dispersal seed predators and might also be affected by selective vegetation removal. Considering this, it is plausible that selective vegetation thinning might in some cases increase seed predation rates, such that this management technique would have negative effects on the regeneration of some tree species. Thus, it is suggested that additional studies assessing the effects of this management technique on seed predation are carried out, particularly for seeds of tree species that are common in mature forest but not in secondary forest.

Under the current scenario of increasing forest destruction and degradation, management techniques will have to be designed and implemented ever more often in order to ameliorate the condition of the remaining forest areas. It is very important, however, that such techniques be applied with some knowledge, not only of their assumed beneficial target effects, but also of their effects on other ecological processes (Guariguata & Pinard 1998). It is also necessary to assess whether such effects will act synergistically or antagonistically with the intended effect of a management manipulation. The results of this study constitute a preliminary basis to suggest that selective vegetation thinning in secondary forests could be recommended as a technique for promoting the establishment of mature forest. However, it remains to be assessed whether other aspects of seed dynamics, such as seed rain and seed germination, also remain unaffected by selective vegetation thinning.

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