The effect of forest successional stage on seed removal of tropical rain forest tree species

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ABSTRACT: Seed removal was evaluated at the macro- and micro-habitat level in areas differing in successional stage in the Bolivian Amazon. The successional stages consisted of secondary forests of 2, 10 and 20 years old and primary forest. Seeds of nine tree species were artificially dispersed and the number of seeds removed was evaluated over 7 weeks. Several stand characteristics were measured at the sites where seeds were dispersed. Seed removal at the end of the experiment varied from 50 to 100% depending on the species, and from 74 to 90% depending on successional stage. In general, the removal rate decreased with an increase in age of successional stage. The seed removal rate was related to liana density and not to litter thickness. Different microhabitat characteristics explained the seed removal rate of four species but microhabitat characteristics did not explain the decrease in seed removal rate with an increase in forest age. The results support the idea that post-dispersal seed removal reduces the number of seeds available for germination, consequently playing an important role in the regeneration of abandoned agricultural areas.

KEY WORDS: Amazon, Bolivia, regeneration, secondary forests, succession

INTRODUCTION

Post-dispersal seed removal may play an important role in determining the composition and density of tree recruitment (De Steven 1991, Hammond 1995, Meiners & Stiles 1997, Myster & Pickett 1993, Uhl et al. 1988, Whelan et al. 1991). The tree species composition can be influenced by seed removal if seed removal agents have a preference for seeds of certain species over others (Harrington et al. 1997, Meiners & Stiles 1997). This preference is related to seed characteristics such as seed size, nutrient content, local abundance and handling time (Meiners & Stiles 1997). Therefore, seed removal agents will
finally determine how many of the seeds dispersed into an area are actually available for germination (Uhl 1987). Although several studies have investigated seed removal rates in closed-canopy forest in comparison to gaps, forest edges or pastures (Dirzo & Dominguez 1986, Holl & Lulow 1997, Sanchez-Cordero & Martínez-Gallardo 1998, Schupp 1988, Schupp & Frost 1989), few studies have assessed seed removal rates in secondary forests differing in successional stage (but see Hammond 1995, Uhl 1987). Tree establishment in areas used for slash-and-burn agriculture is highly dependent on external seed input through dispersal (Uhl 1987), due to the fact that the soil seed bank is reduced during the burning and cultivation of the area (Uhl et al. 1981, Uhl 1987).

As succession progresses in an area, changes occur in forest structure, stem density and plant species composition (Finegan 1984, 1996; Uhl 1987). Because the animal community responds to these changes in the vegetation (Emmons 1982), the composition and abundance of seed removal agents will also vary according to successional stage. Rodents and ants have been reported as the most important seed removal agents in areas undergoing succession (Mittelbach & Gross 1984, Nepstad et al. 1996, Sanchez-Cordero & Martínez-Gallardo 1998, Whelan et al. 1991). Rodents seem to prefer habitats with more cover because cover provides shelter from predators. Predation risk for rodents has been shown to vary as a function of environmental and stand characteristics, such as stand density, type of groundcover (Bowers & Dooley 1993, Brown 1988, Dueser & Shugart 1978, Gill & Marks 1991), and amount of canopy cover (Cassini & Galante 1992, Lagos et al. 1995). It has been reported that younger successional stages have higher ant densities than older ones (Vasconcelos & Cherret 1995).

The objective of this study was to assess the rate of seed removal in forests differing in successional stage, ranging from very young forests (2 y old) to very old ones (mature forest). Our hypotheses were (1) seed removal rate decreases with age of the successional stage; and (2) the removal rate is highest in microhabitats with low litter thickness, high stem and liana density and high plant cover. Seeds dispersed in microhabitats with low litter thickness would be more easily found by seed removal agents than seeds that are dispersed in microhabitats with high litter thickness (Hammond 1995).

METHODS

Research site and study species

The study was carried out in the Bolivian Amazon in El Tigre Forest Reserve (11°5’S, 65°43’W) and in nearby areas owned by local farmers (< 5 km from El Tigre). El Tigre is the research and training centre of the Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), and is located 45 km east of the town of Riberalta. The area receives an annual rainfall of 1780
mm with a dry season (< 100 mm m\(^{-1}\)) from May to September (Beekma et al. 1996). The vegetation of El Tigre and surrounding areas consists mainly of lowland tropical moist forest, with some patches of secondary forests differing in successional stage and agricultural fields. Secondary forest patches are the result of slash-and-burn agriculture and fallow, and often have an area of 1 ha.

Nine tree species were included in the experiment. All of them occur naturally in the area, and differ in their life history strategy, seed weight and fruit characteristics (Table 1). In the text, species will be referred to only by generic name. Once seeds are dispersed, they are likely to be removed by ants (for *Cecropia*, *Cedrela*, *Jacaranda* and *Inga*) and small and large rodents (for *Bertolletia*, *Buchenavia*, *Enterolobium*, *Inga*, *Schizolobium* and *Virola*). Seeds from all species except *Cedrela* and *Schizolobium* were collected in the same area during their natural dispersal period. Fruit flesh was removed except for *Inga*, the seeds of which were offered with a very thin layer of fruit pulp. Seeds of *Cedrela* and *Schizolobium* were obtained from the Centro de Investigación Agrícola Tropical, Santa Cruz, Bolivia. Only undamaged seeds were used in the experiment.

### Table 1. List of tree species used in the experiment, including family name, life history strategy, seed dry weight (in g, mean ± SD), and some fruit characteristics. P, Pioneer; LLP, Long-lived pioneer; C, Climax.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Family</th>
<th>Strategy</th>
<th>Dry weight(^1)</th>
<th>Fruit characteristics(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bertholletia excelsa</em> Humb. &amp; Bonpl.</td>
<td>Lecythidaceae</td>
<td>LLP</td>
<td>6.5 ± 1.5</td>
<td>Woody pyxidium, indehiscent. Opened and dispersed by agoutis.</td>
</tr>
<tr>
<td><em>Buchenavia punctata</em> Eichl.</td>
<td>Combretaceae</td>
<td>C</td>
<td>1.7 ± 0.2</td>
<td>Fleshy drupe. Dispersed by large birds, howler and spider monkeys.</td>
</tr>
<tr>
<td><em>Cecropia sciadophylla</em> Mart.</td>
<td>Moraceae</td>
<td>P</td>
<td>0.0018 ± 0.0008</td>
<td>Fleshy spikes, fruit: small achenes. Dispersed by all monkeys, bats, toucans, tayras.</td>
</tr>
<tr>
<td><em>Cedrela odorata</em> L.</td>
<td>Meliaceae</td>
<td>LLP</td>
<td>0.036 ± 0.013(^2)</td>
<td>Capsule, indehiscent (winged seed). Dispersed by wind.</td>
</tr>
<tr>
<td><em>Enterolobium contortisiliquum</em> Morong.</td>
<td>Mimosaceae</td>
<td>C</td>
<td>4.1 ± 0.5</td>
<td>Woody legume, indehiscent. Dispersed by howler monkeys.</td>
</tr>
<tr>
<td><em>Inga</em> sp.</td>
<td>Mimosaceae</td>
<td>LLP</td>
<td>3</td>
<td>Legume, indehiscent, seeds covered with white mesocarp. Dispersed by spider and howler monkeys.</td>
</tr>
<tr>
<td><em>Jacaranda copia</em> D.Don</td>
<td>Bignoniaceae</td>
<td>LLP</td>
<td>0.005 ± 0.003(^2)</td>
<td>Capsule, indehiscent (winged seed). Dispersed by wind.</td>
</tr>
<tr>
<td><em>Schizolobium amazonicum</em> Huber ex Ducke</td>
<td>Caesalpiniaceae</td>
<td>P</td>
<td>0.92 ± 0.15</td>
<td>Samara-like legume, late indehiscent (single seed).</td>
</tr>
<tr>
<td><em>Virola sebifera</em> Aubl.</td>
<td>Myristicaceae</td>
<td>C</td>
<td>1.4 ± 0.2</td>
<td>Capsule, indehiscent (seed covered with red aril).</td>
</tr>
</tbody>
</table>

\(^1\) All seeds were dried in an oven for two days (80 °C) before weighing with the exception of seeds of *Cecropia*. Weight of *Cecropia* is fresh weight.

\(^2\) Seed without wings.

\(^3\) Data not available because of insufficient seeds.

\(^4\) Information in parentheses refers to seed type. Information regarding seed dispersal based on van Roosmalen (1985).
Experimental design

From mid April to end May 1998 we measured seed removal from experimental seed depots, mimicking clumps of dispersed seeds, in four successional stages: secondary forests of 2, 10 and 20 y and mature forests. We selected two sites per successional stage that were highly similar in vegetation structure. Site age was determined by interviewing the owners of the sites and long-term residents of the area. In each site, five parallel transects were established, 10–20 m apart from each other. Along the transects, nine seed depots were established at 8-m intervals, giving a total of 360 depots. We used seed depots to prevent seeds from being washed away during heavy rains. The seed depots had a triangular shape (20 cm per side), were made of green nylon mosquito netting with a mesh of 1 mm, and had the edges of the triangle (3 cm) folded upright. Seed depots were fixed to the ground at each corner by cramps made of 12-cm-long pieces of iron wire. Seed depots did not influence the foraging behaviour of the animals; in a trial experiment, seeds placed directly on the forest floor showed the same removal rate as seeds placed in the seed depots (data not shown). Species were randomly assigned to the seed depots of a given transect, on the condition that seeds of the same species were not next to each other in two adjacent transects.

Fifty seeds of *Cecropia* and 12 seeds of all other species were evenly distributed over the seed depots. More seeds of *Cecropia* were used because of their small size. Depots were checked after 2, 7, 14, 21, 35 and 49 d of seed placement. On each evaluation day the number of seeds inside and within 10 cm of the seed depot was counted as seeds still present. Seeds eaten in the depot were considered as removed seeds. Litter falling into the seed depots was removed periodically. We walked between two transects (three per site) during the visits; thus, reducing damage to the surrounding vegetation close to the seed depots.

During the seed removal evaluation period several stand characteristics were evaluated in a 1-m radius around half of the seed depots at each site, providing a total of 180 depots. The stem density was estimated by counting all plants > 10 cm in height. In the case of multi-stemmed plants each stem was counted individually. The liana density was evaluated separately from stem density by counting all the lianas rooted in the circle or passing through it. Lianas are an important life form in early successional stages and give a more dense structure to the forest. In addition, the area of the circle covered by herbs and other plants < 30 cm in height (referred hereafter as plant cover) and the area covered by dead *Cecropia* leaves were estimated (in %). The area covered by dead *Cecropia* leaves (referred hereafter as *Cecropia* litter cover) was evaluated because *Cecropia* litter is a conspicuous feature in the understorey of successional stages dominated by this species. The leaf litter thickness was evaluated in eight different places of the circle by determining the number of leaf layers intersected by a knifepoint. Stem and liana densities were calculated as
number of individuals m\(^{-2}\). The leaf litter thickness of a given circle was estimated by calculating the median value of the eight points measured per circle.

To assess the mammal community present at the sites, three 1-m × 1-m footprint traps were established in each site at random locations. The vegetation of the footprint traps was removed and the ground softened with a machete to get a smooth surface. Plots were checked for animal tracks every week for 2 mo (May–June 1998). Tracks were identified to the lowest possible level by local people.

Data analysis

Differences in stem density among successional stages were analysed with a one-way ANOVA. The Student–Newman–Keuls test was used as a post-hoc test. Data on liana density, plant cover, *Cecropia* litter cover, and leaf litter thickness had unequal variances, so for these variables Kruskall–Wallis tests were used with successional stage as factor. To find differences between pairs of successional stages, the Kruskall–Wallis test was performed several times. The P value was corrected accordingly using the Bonferroni correction (P value: 0.0083).

Seed removal data were analysed with a survival analysis (Fox 1993). The effect of successional stage on seed removal rate was determined for all species together and for each species using Cox regression. For the analysis we used the day of census in which we visited the depots, and we pooled seed depots per species and per successional stage. Simple contrasts were carried out to find significant differences among the different successional stages. There were six possible contrasts; consequently, the P value was corrected using a Bonferroni correction (P value: 0.0083).

To evaluate the effect of microhabitat on seed removal, the seed removal rate was calculated per seed depot. For each individual seed depot, the removal rate was estimated by regressing the log-number of removed seeds (x + 1) against time. The removal rates obtained per seed depot were then regressed against the corresponding stand characteristics, using a forward stepwise multiple regression analysis. This analysis was also performed for each species and for all species combined.

RESULTS

All stand characteristic parameters except leaf litter thickness varied significantly with successional stage (Figure 1). Stem density was lower in the 2- and 10-y-old secondary forests and higher in the mature forest (Figure 1a), while liana density showed the opposite trend (Figure 1b). The plant cover was lowest in the 10-y-old secondary forest and highest in the mature forests (Figure 1c). The *Cecropia* litter cover was significantly higher in the 10-y-old secondary forests, and no *Cecropia* litter cover was found in the mature forest (Figure 1d).

Most of the depots (66%) were visited within the first 7 d of the experiment.
Seed removal after 7 wk varied from 48% for *Buchenavia* to 100% for *Cedrela*, and from 74% for the mature forest to 90% for the 2-y-old secondary forest (Table 2). The successional stage had an effect on seed removal rate for all species but *Bertholletia* (Table 2, Figure 2). Most species experienced the highest removal rate in the 2-y-old secondary forests, while *Cecropia* did in the 10-y-old secondary forest. The lowest removal rate was found in the mature forest for *Buchenavia*, *Cecropia*, *Enterolobium*, *Inga*, *Jacaranda* and *Schizolobium*. *Cedrela* had the lowest removal rate in the 20-y-old secondary forest and *Virola* in the 10-y-old secondary forest (Table 2, results of contrasts).

The seed removal rate of *Bertholletia*, *Buchenavia*, *Inga* and *Virola* were only
Successional stage and seed removal in Bolivia

Table 2. Results of the Cox regression analysis testing for effect of successional stage on the removal rate over all species and per species. Also shown are the results of the contrasts among different successional stages and the removal percentage per species and per successional stage at day 49 (end of experiment). Successional stages followed by the same letter are not significantly different (at $P = 0.0083$). $2\,y$ = 2-y-old secondary forest, $10\,y$ = 10-y-old secondary forest, $20\,y$ = 20-y-old secondary forest, MF = mature forest.

<table>
<thead>
<tr>
<th>Species</th>
<th>$P$</th>
<th>Successional stages</th>
<th>Removal percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2 y</td>
<td>10 y</td>
</tr>
<tr>
<td>All species</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td>Bertholletia</td>
<td>0.6292</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Buchenavia</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Cecropia</td>
<td>&lt; 0.001</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Cedrela</td>
<td>0.0011</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Enterolobium</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Inga</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>ab</td>
</tr>
<tr>
<td>Jacaranda</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Schizolobium</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Virola</td>
<td>0.0177</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Removal percentage</td>
<td></td>
<td>89.6</td>
<td>86.3</td>
</tr>
</tbody>
</table>

Removal percentage of Bertholletia, Inga and Virola decreased as the leaf litter thickness, the Cecropia litter cover and the liana density increased, respectively (Table 3, Figure 3). The removal rate of Buchenavia varied with liana density and plant cover (Table 3). For a list of mammals present in the different sites based on tracks found in the footprint traps see Table 4.

DISCUSSION

In this study the final fate of the removed seeds was not evaluated. It is likely that some of the removed seeds were cached by rodents (Brewer & Rejmánek 1999; Forget 1990, 1993) or deposited intact on refuse piles by ants (Levey & Byrne 1993) rather than immediately eaten. In the case of rodent-removed seeds, a large variation in the percentage of seeds cached has been found (ranging 0–92%), depending on season of the year, resource availability and removal agent (Brewer & Rejmánek 1999 and references therein; Forget 1990, 1993). The few studies that have looked at the ultimate fate of cached seeds have, however, reported very low numbers of finally established seedlings (2 seedlings out of 923 seeds (Wenny 2000), and 1 seedling out of 489 seeds (Jansen et al. in press)). If we assume that the results of the above-mentioned studies also apply to our sites, then the removal rates we found provide an approximation of the amount of seeds that is lost from the moment the seeds are dispersed to the area to the moment a seedling gets established. The general trend found in this study was a decrease in seed removal rate with an increase in forest age. For this trend to be reversed, seeds removed in the younger successional stages would need to have a higher probability of establishing than seeds removed in older successional stages. Species, however, show an optimum in germination and post-germination survival rates at different
Figure 2. Removal rate of the different species by successional stage. Data presented are mean of two sites per successional stage. MF = mature forest.
Table 3. Effect of microhabitat characteristics on the removal rate per species and over all species. Removal rate is calculated by seed depot using a linear regression. A forward stepwise multiple regression analysis was performed. Slopes for the different stand characteristics included in the regression models are given. NS, non-significant.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Stem density</th>
<th>Leaf density</th>
<th>Ceropía litter cover</th>
<th>Plant cover</th>
<th>Leaf litter thickness</th>
<th>r²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bertholletia</td>
<td>27</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Buchenavia</td>
<td>17</td>
<td>—</td>
<td>0.0271</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.184</td>
<td>0.025</td>
</tr>
<tr>
<td>Cecropia</td>
<td>25</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.380</td>
<td>0.002</td>
</tr>
<tr>
<td>Cedrela</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>NS</td>
<td>—</td>
</tr>
<tr>
<td>Enterolobium</td>
<td>22</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>NS</td>
<td>—</td>
</tr>
<tr>
<td>Inga</td>
<td>15</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.443</td>
<td>0.009</td>
</tr>
<tr>
<td>Facaranda</td>
<td>14</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>NS</td>
<td>—</td>
</tr>
<tr>
<td>Schizolobium</td>
<td>23</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>NS</td>
<td>—</td>
</tr>
<tr>
<td>Virola</td>
<td>19</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.280</td>
<td>0.035</td>
</tr>
<tr>
<td>All species</td>
<td>180</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>NS</td>
<td>—</td>
</tr>
</tbody>
</table>

Successional stage and seed removal in Bolivia

Seven wk after seeds had been artificially dispersed, 85% had been removed. The removal ranged from almost 50 to 100% depending on the species, and from 74 to 90% depending on the successional stage (Table 2). This range is similar to the values reported for other tropical regions. For example, secondary forests of different ages and primary forest: 98.4% over 2 m (Hammond 1995); 2-yr-old secondary forest and gaps in primary forest: 35–100% over 4 m (Uhl 1987); closed-canopy forests vs. gaps: 97% over 20 wk (Cintra & Horna 1997); pastures and gaps in primary forest: > 80% for eight of 11 species over 50 d (Nepstad et al. 1996); pastures, gaps in primary forest, forest edge and canopy closed forest: 59% over 1 m (Osunkoya 1994). For species with low removal rates (Buchenavia and Jacaranda, see Table 2), it seems that depots were not detected or were detected but seeds ignored (15% of all depots containing Buchenavia and 7.5% of those containing Jacaranda still had all seeds present at the end of the experiment). The low removal of Buchenavia could be due to the fact that the seeds were offered without fruit pulp and that the seeds are surrounded by a very thick pericarp.

In general, removal rate decreased as the age of the forests increased (Table 2, Figure 2). Lower seed removal rates in older successional stages than in younger ones have been related to the thickness of the litter layer (Hammond 1995). The line of reasoning is that the older the successional stage the higher the amount of litter, and therefore, the higher the chances of the seeds not being found by seed removal agents. In this study, however, leaf litter thickness did not increase with forest age (Figure 1e), probably because of the season in which measurements were conducted (end of rainy season). Other studies have found an increase in seed removal rate with an increase in stem and liana.
Figure 3. Examples of the relationship between removal rate and stand characteristics. (a) The removal rate of *Inga* is related to *Cecropia* litter cover and (b) the removal rate of *Virola* is related to liana density. For regression coefficients and \( r^2 \) values see Table 3.

Table 4. Granivorous mammals in the different successional stages, based on tracks found in footprint traps. ×, present; —, not present.

<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>2-y-old</th>
<th>10-y-old</th>
<th>20-y-old</th>
<th>Mature forest</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dasyprocta</em> spp. (agouti)</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Agouti paca</em> (paca)</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>rats</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>—</td>
</tr>
<tr>
<td><em>Mazama</em> spp. (deer)</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
</tbody>
</table>
density, vegetation structure and ground cover (Manson & Styles 1998, Myster & Pickett 1993, Osunkoya 1994). In this study, however, the lowest seed removal rate was found in the mature forest (Table 2), which had the highest stem density and the highest plant cover of all successional stages (Figure 1a, d). Based on these results, the decrease in seed removal rate with an increase in forest age seems to be related to a decrease in liana density as the forest becomes older (Figure 1b).

Microhabitat characteristics only partly explained the seed removal rate of Bertholletia, Buchenavia, Inga and Virola (Table 3, Figure 3). As predicted, seeds of Bertholletia, Inga and Virola had higher probabilities of surviving when dispersed in microhabitats that reduce their chances of being found, i.e. microhabitat that had higher leaf litter thickness, more Cecropia litter cover and higher liana density, respectively. On the other hand, Buchenavia seeds had a higher chance of surviving in areas with low liana density and high plant cover (Table 3). These different microhabitats are not unique to a given successional stage; i.e. there is microhabitat heterogeneity within a successional stage. Our results clearly demonstrate that microhabitat per se cannot explain the general trend that younger stages of succession have a higher removal rate than older ones. This heterogeneity, however, may play a crucial role in the regeneration of secondary forests because it may allow seeds of preferred species to escape removal (sensu Mittelbach & Gross 1984).

The decrease in seed removal rate with age of the forest should ultimately be related to lower abundance of removal agents. Ants in general and granivorous ants in particular (such as Atta, Solenopsis, Wasmannia; Kaspari 1995, Vasconcelos & Cherret 1995) have been found to be more abundant in younger secondary forests than in older ones. Studies conducted in our research site have also found the pattern described above (R. Dunn, pers. comm.). The higher ant abundance in younger successional stages has been related to a higher productivity and a higher abundance of open areas for nest establishment in these stages than in older ones (Vasconcelos & Cherret 1995). Rodent abundance is likely to vary also with successional stage. Data available in the literature, however, are scarce and sometimes contradictory (Estrada et al. 1998, Medellín & Equihua 1998, Nepstad et al. 1996). Variation in rodent abundance in different successional stages may also depend on the taxa considered. For example, Dasyprocta spp. (large rodents) forage both in open and closed forests (P. M. Forget, pers. comm.); therefore, they may be equally abundant in young and old successional stages. Dasyprocta spp. are the major removal/dispersal agent of Bertholletia (Peres et al. 1997), which interestingly enough was the only species equally removed in all successional stages (Table 2, Figure 2). The hypothesis, however, that the decrease in seed removal rate with age of the forest is due to a decrease in rodent density can not be tested with this study. This hypothesis deserves further investigation, given the fact that a relation between seed removal rates and rodent community has been found in other studies (Asquith et al. 1997, 1999; Hoch & Adler 1997).
Our results support the idea that post-dispersal seed removal plays an important role in the establishment of trees in abandoned agricultural areas because seed removal largely reduces the amount of seeds available for germination. Combining the data of this study with data of other studies on germination and early seedling survival that were carried out in the same sites and with the same species, it was found that the final number of seedlings established was highly influenced by seed removal (Peña-Claros 2001). This has also been found for Ocotea endresiana, a montane tree species in Costa Rica (Wenny 2000).

Seed removal rates decrease with an increase in forest age, so that seeds dispersed to younger stages of succession have lower chances of surviving than seeds dispersed to older ones. This result has different implications for species differing in shade tolerance. Pioneer species have their recruitment restricted to very young successional stages or large gaps in primary forest because they require high light levels for their establishment (Kyereh et al. 1999, Peña-Claros 2001). They may compensate for the higher seed removal rate in young successional stages by a high and continuous fruit production. Shade tolerant species, on the other hand, are known to establish themselves slowly and continuously in areas undergoing succession. This may be due to the fact that they have different establishment requirements than pioneer tree species (Finegan 1984, Uhl 1987) or that their seeds arrive at the area in smaller quantities than the seeds of pioneer species (Uhl 1987, Uhl et al. 1981). The latter combined with a higher seed removal rate in younger successional stages may explain the lower density of mature forest tree seedlings found in young successional stages (Uhl et al. 1981).

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