Chapter 3

The effect of successional stage on seed removal of tropical rainforest tree species

with Henneleen de Boo

Abstract

Seed removal was evaluated at the macro and microhabitat in areas differing in successional stage in the Bolivian Amazon. The successional stages consisted of secondary forests of 2, 10 and 20 years and primary forest. Seeds of nine tree species were artificially dispersed into the different successional stages and the number of seeds removed was evaluated during seven weeks. Several stand characteristics were evaluated 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. Different microhabitat characteristics explained the removal rate of four species but did not explain the pattern in seed removal rate observed. The higher seed removal rate in young secondary forests seems to be related to the density of seed removal agents, which apparently both in the case of ants and rodents decreases with forest age. The results support the idea that post-dispersal seed removal plays an important role in the establishment of trees in abandoned agricultural areas.
Introduction

Tree establishment in areas used for slash-and-burn agriculture is highly dependent on seed dispersal (Uhl 1987), due to the fact that the soil seed bank has been largely reduced during the burning and farming of the area (Uhl et al. 1981, Uhl 1987). Consequently, post-dispersal seed removal may play an important role in determining the tree species composition and tree density of an area undergoing succession (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 rates if the seed removal agents have a preference for seeds of certain species over others. Moreover, seed removal agents will finally determine how many seeds of the seeds dispersed into an area are actually available for germination (Uhl 1987). Although several studies have studied seed removal rates in closed canopy forest in comparison to gaps, forest edges or pastures (e.g. Dirzo & Dominguez 1986, Holl & Lulow 1997, Schupp 1988, Schupp & Frost 1989, Sanchez-Cordero & Martínez-Gallardo 1998), very few studies have assessed seed removal rates in secondary forests differing in successional stage (but see Hammond 1995, Uhl 1987).

As succession progresses in an area, several changes occur in terms of forest structure, stem density and plant species composition (Finegan 1984 and 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 (e.g. Mittelbach & Gross 1984, Whelan et al. 1991, Nepstad et al. 1996, Sanchez-Cordero & Martínez-Gallardo 1998). Rodents seem to prefer habitats with more cover because cover provides them shelter from predators. Predation risk for rodents has been shown to vary as a function of several 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). There is little information available on the habitat preference of ants, although higher ant densities have been reported for younger successional stages than for older ones (e.g. Vasconcelos & Cherret 1995).

Seed removal agents have been shown to prefer seeds of certain species to all the seeds available in the community, limiting in that way the
establishment of the preferred species (cf. Meiners & Stiles 1997). This preference may be related to seed characteristics such as seed size, nutrient content, local abundance, and handling time (Meiners & Stiles 1997). Some authors have found a negative relationship between seed removal rate and seed size (Nepstad et al. 1996, Osunkoya 1994, Uhl 1987), which implies that large seeded species would have a higher chance of being present in secondary forests than small seeded species. Others studies have found, however, no relationship between removal rate and seed size (Holl & Lulow 1997, Meiners & Stiles 1997, Myster & Pickett 1993).

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 year old) to very old ones (mature forest). Our hypotheses were 1) seed removal rate will decrease with age of the successional stage; 2) given that stand characteristics vary with successional stage, the seed removal rate observed will depend on stand characteristics. We expect that removal rate will be higher in microhabitats with low litter thickness, high stem and liana density, and high plant cover than in microhabitats with opposite characteristics; and 3) small seeded species will have a higher seed removal rate than large seeded species (see Fig. 1 for schematic model of the hypotheses). In this paper, we used the term “seed removal” instead of “seed predation” because we did not assess the final fate of the seed after being removed from the seed depots (predated or dispersed to another site). The probability, however, that most seeds removed will be finally predated is high. Only about 6.4 % of the seeds removed by ants are deposited intact on refuse piles (Levey & Byrne 1993), and seeds cached by rodents have also a high probability of being predated later on (Price & Jenkins 1986).

![Fig. 1. Model showing the different factors that may affect the removal rate of seeds in successional stages differing in age.](image-url)
Methodology

Research site and study species

The study was carried out in the Bolivian Amazon in the forest reserve El Tigre (11°59’S, 65°43’W) and in nearby areas owned by local farmers (< 5 km from El Tigre). El Tigre is the research and training center 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/month) from May to September (Beekma et al. 1996). The vegetation of El Tigre and surrounding areas consist 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, dispersal mode and removal agent (Table 1). Henceforth, species will be referred to only by generic name.

Experimental design

The study was carried out in 4 successional stages: secondary forests of 2, 10 and 20 years and mature forests. Two sites were selected per successional stage. Site selection was based on similarities in vegetation structure between sites of the same successional stage. Site age was determined by interviewing the owners of the sites and long term residents of the area.

In each site, five transects were established in the center of the secondary forest, each transect at least 10 m apart from each other. Along the transects, nine seed depots were laid out, each seed depot spaced 8 m apart. The seed depots had a triangular shape (20 cm per side) and were made of green colored nylon mosquito netting with a mesh of 1 mm. To prevent seeds from being washed away from the seed depot during heavy rains, the edges of the triangle (3 cm) were folded upright. Seed depots were fixed to the ground at each corner by cramps made of 12 cm long pieces of iron wire. Species were randomly allocated 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. In a trial experiment, seed depots did not have a positive or negative influence on the foraging behaviour of the animals. Seeds placed directly on the forest floor showed the same removal rate as seeds placed in the seed depots (data not shown).
Seeds from all species except Cedrela and Schizolobium were collected in the same area during their natural dispersal period. Fruit flesh was removed in all cases but Inga, which seeds 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. Twelve seeds of a given species were evenly distributed in the corresponding seed depot. In the case of Cecropia, 50 seeds were placed per depot because of its small seed size. Depots were checked after 2, 7, 14, 21, 35 and 49 days of seed placement. At each evaluation day the number of seeds inside and within 10 cm of the seed depot were counted as seeds still present. Seeds eaten in the depot were considered as removed seeds. Litter falling into the seed depots was removed periodically. Walking paths constructed between two transects (three per site) were used during the check up; thus, reducing damage to the surrounding vegetation.

Several stand characteristics were evaluated in a 1 m radius around half of the seed depots at each site, providing a total of 179 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, in %) and the area covered by dead Cecropia

Table 1. List of tree species used in the experiment. Family name, life history strategy, seed dry weight (mean ± SD), dispersal mode, and removal agent are given. P = Pioneer, LLP = Long-lived Pioneer, C = Climax.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Family</th>
<th>Strategy</th>
<th>Dry weight (g)</th>
<th>Dispersal mode</th>
<th>Removal agent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bertholletia excelsa</td>
<td>Lecythidaceae</td>
<td>LLP</td>
<td>6.508 ± 1.476</td>
<td>zoocorous</td>
<td>rodents</td>
</tr>
<tr>
<td>Buchenavia punctata</td>
<td>Combretaceae</td>
<td>C</td>
<td>1.712 ± 0.197</td>
<td>zoocorous</td>
<td>rodents</td>
</tr>
<tr>
<td>Cecropia sciadophylla</td>
<td>Moraceae</td>
<td>P</td>
<td>0.0014</td>
<td>zoocorous</td>
<td>ants</td>
</tr>
<tr>
<td>Cedrela odorata</td>
<td>Meliaceae</td>
<td>LLP</td>
<td>0.036 ± 0.013</td>
<td>anemochorous</td>
<td>ants</td>
</tr>
<tr>
<td>Enterolobium contortisiliquum</td>
<td>Mimosaceae</td>
<td>C</td>
<td>4.060 ± 0.498</td>
<td>zoocorous</td>
<td>rodents</td>
</tr>
<tr>
<td>Inga spp.</td>
<td>Mimosaceae</td>
<td>LLP</td>
<td>0.005 ± 0.003</td>
<td>anemochorous</td>
<td>ants</td>
</tr>
<tr>
<td>Jacaranda copaia</td>
<td>Bignoniaceae</td>
<td>LLP</td>
<td>0.921 ± 0.148</td>
<td>zoocorous</td>
<td>rodents + ants</td>
</tr>
<tr>
<td>Schizolobium amazonicum</td>
<td>Caesalpinaceae</td>
<td>P</td>
<td>1.410 ± 0.191</td>
<td>zoocorous</td>
<td>rodents</td>
</tr>
<tr>
<td>Virola sebifera</td>
<td>Myristicaceae</td>
<td>C</td>
<td>0.005 ± 0.003</td>
<td>anemochorous</td>
<td>ants</td>
</tr>
</tbody>
</table>

1 Seeds were dried in an oven for two days (80 °C) before weighing.
2 Seed without wings.
3 Data not available due to restriction in number of seeds.
4 Based on literature and personal observations.
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 understory of successional stages dominated by this species. The leaf litter thickness was evaluated in eight different places of the circle by determining the amount of leaf layers intersected by a knifepoint. Stem and liana densities were calculated as number of individuals per m². The leaf litter thickness of a given circle was estimated by calculating the median value of the eight points measured per circle.

**Data analysis**

Differences in stem density among successional stages were analysed with a one-way ANOVA. The Student-Newman-Keuls test was used as post-hoc test. Data on liana density, plant cover, Cecropia litter cover, and leaf litter thickness data 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. 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 for contrasts is 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 ln-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 done per species and overall species.

The effect of seed size on removal rate was analysed at two levels. First, the species specific removal rate averaged over all successional stages was regressed on seed weight. Second, we regressed the specific removal rates of a given successional stage against seed weight. Removal rate was calculated per seed depot as indicated in the above paragraph.
Results

All stand characteristics but leaf litter thickness varied with successional stage (Fig. 2). Stem density was lower in the 2 and 10 year old secondary forests and higher in the mature forest (Fig. 2A), while liana density showed the opposite trend (Fig. 2B). The plant cover was lowest in the 10 year old secondary forest and highest in the mature forests (Fig. 2C). The *Cecropia* litter cover was significantly higher in the 10 year old secondary forests, and no dead *Cecropia* leaves were found in the mature forest (Fig. 2D).

After seven weeks the seed removal varied from 48.3 % for *Buchenavia* to 99.8 % for *Cedrela*, and from 74 % for the mature forest to 90 % for the 2 year old secondary forest (Table 2). For all species but *Bertholletia* the successional stage had an effect on seed removal rate (Table 2, Fig. 3). Most species experienced the highest removal rate in the 2 year old secondary forests, while *Cecropia* did in the 10 year 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 year old secondary forest and Virola in the 10 year old secondary forest (Table 2, results of contrasts).

The seed removal rate of Bertholletia, Buchenavia, Inga and Virola were only partially explained by the different microhabitat characteristics (Table 3). The removal rate of Bertholletia, Inga and Virola decreased as the leaf litter
thickness, the *Cecropia* litter cover and the liana density increased, respectively (Table 3, Fig. 4). The removal rate of *Buchenavia* varied with liana density and plant cover (Table 3).

No relationship between average seed removal rate and seed mass was found (Linear regression, \( p = 0.77 \)). Neither was there a relationship between seed removal rates of specific successional stages and seed mass (Linear regression; for 2 year secondary forest: \( p = 0.19 \); for 10 year secondary forest: \( p = 0.97 \), for 20 year secondary forest: \( p = 0.54 \), and for mature forest: \( p = 0.71 \)).

### 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 in a given row followed by the same letter are not significantly different (at \( p = 0.0083 \)). 2 y = 2 year old secondary forest, 10 y = 10 year old secondary forest, 20 y = 20 year old secondary forest, MF = mature forest.

<table>
<thead>
<tr>
<th>Species</th>
<th>p value</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>92.3</td>
<td></td>
</tr>
<tr>
<td>Buchenavia</td>
<td>&lt; 0.0001</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Cecropia</td>
<td>&lt; 0.0001</td>
<td>b</td>
<td>a</td>
</tr>
<tr>
<td>Cedrela</td>
<td>0.0011</td>
<td>a</td>
<td>ab</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>a</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>
</tbody>
</table>

Removal percentage 89.6 86.3 84.9 74.0

Fig. 4. Examples of the relationship between removal rate and stand characteristics. The removal rate of *Inga* and *Virola* is related to *Cecropia* litter cover and liana density, respectively. For equation and \( r^2 \) see Table 3.
Seven weeks 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 (e.g., secondary forests of different ages and primary forest: 98.4% over 2 months (Hammond 1995); 2 year old secondary forests and gaps in primary forest: 35-100% over 4 months (Uhl 1987); closed canopy forests vs. gaps: 97% over 20 weeks (Cintra & Horna 1997); pastures and gaps in primary forest: > 80% for eight of 11 species over 50 days (Nepstad et al. 1996); pastures, gaps in primary forest, forest edge, and canopy closed forest: 59% over one month (Osunkoya 1994)). Most of the depots were visited within the first 7 days of the experiment, so that after only one week just 34% of all depots had all seeds present (Fig. 3). 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 have a very thick pericarp.

In general, removal rate decreased as the age of the forests increased. For all species except *Bertholletia* the removal rate varied among successional stages (Table 2, Fig. 3). This result can be related to differences in abundance of removal agents, i.e., ants and rodents. The pattern of a higher removal rate

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**Table 3. Effect of microhabitat characteristics on the removal rate per species and over all species.**

A forward stepwise multiple regression analysis was performed. The 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>liana density</th>
<th>Cecropia litter cover</th>
<th>plant cover</th>
<th>leaf litter thickness</th>
<th>r²</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bertholletia</em></td>
<td>27</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-0.0107</td>
<td>0.184</td>
<td>0.025</td>
</tr>
<tr>
<td><em>Buchenavia</em></td>
<td>17</td>
<td>-</td>
<td>-0.0271</td>
<td>-</td>
<td>-0.00056</td>
<td>-</td>
<td>0.580</td>
<td>0.002</td>
</tr>
<tr>
<td><em>Cecropia</em></td>
<td>25</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td><em>Cedrela</em></td>
<td>18</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td><em>Enterolobium</em></td>
<td>22</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td><em>Inga</em></td>
<td>15</td>
<td>-</td>
<td>-</td>
<td>-0.00053</td>
<td>-</td>
<td>-</td>
<td>0.443</td>
<td>0.009</td>
</tr>
<tr>
<td><em>Jacaranda</em></td>
<td>14</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td><em>Schizolobium</em></td>
<td>23</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td><em>Virola</em></td>
<td>19</td>
<td>-</td>
<td>-</td>
<td>-0.0045</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>
in younger stages (2 and 10 year old) than in older ones (20 years old and mature forest) observed for seed removed by ants (*Cecropia*, *Cedrela* and *Jacaranda*) is likely to be due to differences in ant density among successional stages. A higher abundance of ants in general, and of granivorous ants in particular (such as *Atta*, *Solenopsis*, *Wasmannia*; Kaspari 1995, Vasconcelos & Cherret 1995), has been found in younger secondary forests as compared to older ones. Studies done in our research site have also found the pattern described above (Robert Dunn, personal communication). The higher ant abundance in younger secondary forests has been related to a higher productivity and a higher abundance of open areas for nest establishment in these forests than in older successional stages (Vasconcelos & Cherret 1995).

Removal rates of seeds removed by rodents have been related to the density and the behaviour of rodents (e. g. Osunkoya 1994, Asquith et al. 1997, Manson & Stiles 1998, Sanchez-Cordero & Martinez-Gallardo 1998) and to stand characteristics (e. g. Hammond 1995, Whelan et al. 1991, Manson & Styles 1998). In this study all species removed by rodents but *Bertholletia* were removed at a higher rate in the younger successional stages than in the older ones (Table 2), suggesting that there is a higher density of rodents in younger stages than in older ones. Densities of mammal footprints, however, were not significantly different among the different successional stages (H. de Boo, unpublished data). The evidence available so far is the literature on rodent density in different successional stages is scarce and sometimes contradictory. It has been reported that there is no difference in terms of mammal abundance and species richness between 6 year old secondary forests and mature forests (Medellin & Equihua 1998), that there is a higher abundance of rodents in pastures when compared to mature forests (Nepstad et al. 1996), and that pastures have lower abundance of non-flying mammals than forest, forest edges and plantations (Estrada et al. 1998).

Rodents seem to prefer habitats that allow them to reduce the risk of being predated (e. g. Manson & Stiles 1998). Lower seed removal rates in older successional stages than in younger ones have been related to the thickness of the litter layer. 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 to be found by seed removal agents (Hammond 1995). In this study, however, leaf litter thickness did not increase with age of the forest (Fig. 2E). Other studies have found an increase in seed removal rate with an increase in stem and liana density, vegetation structure and ground cover (Myster & Pickett 1993, Osunkoya 1994, Manson & Styles 1998). 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 (Fig. 2A and 2D). Based on these results, the general trend observed is apparently mainly due to a decrease in liana density as the forest age increases (Fig. 2B). Young successional stages are characterized by a high abundance of lianas, which gives a more dense structure to the forest. Rodents may have a smaller risk of being predated while foraging in these areas than in older successional stages, and therefore, the seed removal rate is higher than in older successional stages.

The seed removal rate observed could only be partly explained by microhabitat characteristics in the case of *Bertholletia, Buchenavia, Inga* and *Virola* (Table 3, Fig. 4). Apparently 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 can not 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).

Seeds of *Bertholletia, Buchenavia* and *Virola* are more likely to be removed by rodents than by ants because of their seed size (Table 1). The fact that only their seed removal rates were partly explained by microhabitat characteristics suggests that the stand characteristics evaluated in this study may not serve as cues for seed removal by ants. This is probably related to differences in the way that rodents and ants perceive their environment because of body size constraints (Kaspari & Weiser 1999). Another explanation for these results could be the difference in foraging behavior between ants and rodents. For many ants, the discovery of seeds is mainly dependent on whether the seeds are within the vicinity of the foraging trails (Mull & Macmahon 1997), while in the case of rodents it is mainly dependent on territorial behavior and predator avoidance (Bowers & Dooley 1993).

Seed removal rate was not related to seed mass, as has been reported by other studies (e.g. Holl & Lulow 1997). Seeds were removed by different seed removal agents (Table 1) that use different strategies for seed removal and that
may differ in their densities. In the case of seeds removed by ants, the relationship becomes unclear because big seeds are likely to attract bigger ants as well as mass recruiting species (Robert Dunn, personal communication). Consequently, small and large seeds may have an equal chance of being removed. In the case of seeds removed by rodents, no relation was found between seed removal rate and seed mass even when only rodent-removed species were considered (data not shown).

As predicted in our model (Fig. 1), seed removal rate decreases as the age of the successional stage increases (Table 2). It is not, however, influenced by stand characteristics (Table 3) or by seed size. This suggests that other stand characteristics than the ones measured in this study are determining the effect of successional stage on seed removal rate. In the case of seeds removed by ants, the effect of successional stage on seed removal may be explained by a decrease in ant density with an increase in age of successional stage (e.g. Kaspari 1995, Vasconcelos & Cherret 1995, R. Dunn, personal communication). In the case of seeds removed by rodents, the effect of successional stage on seed removal rate may as well be explained by the density of the removal agent. If we assume that the abundance of rodents is higher in areas with more dense vegetation because the risk of being predated decreases, then we can expect a higher removal rate in younger successional stages than in older ones. Additionally, we can expect that in the older successional stages there would be a greater selectivity of resources (less preferred species would have lower seed removal rates than highly preferred species) because rodent density would be lower (P. Jansen, personal communication).

The results of this study support the idea that post-dispersal seed removal plays a role in the establishment of trees in abandoned agricultural areas. 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 has different implications for tree species differing in shade tolerance. Shade tolerant species are known to establish themselves slowly in areas undergoing succession. This may be due to the fact that they have other establishment requirements than pioneer species (Uhl 1987, Finegan 1984) or that their seeds arrive to the area in smaller quantities than the seeds of pioneer species (Uhl et al. 1981, Uhl 1987). The latter case combined with a higher seed removal rate in younger stages of succession may explain better the low density of forest tree seedlings found in young successional stages (Uhl et al. 1981). Pioneer and long-lived pioneer species, on the other hand, get established in higher densities in younger successional stages. These species need to be dispersed to early stages of succession to encounter the high light
levels necessary for their establishment (Kyereh et al. 1999, Guariguata 2000, Chapter 4). Therefore, they should be able to overcome the high seed removal rates typical of younger stages of succession. A massive seed production, a seed production throughout the year, a high seed dispersal rate, and/or a quick germination after dispersal may help compensate the high seed removal values found in early stages of succession.

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