

Effect of bromeliad (*Pseudananas sagenarius*) cover on seed predation and tree regeneration in tropical dry forest INPA, Bolivia



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Summary

Dry tropical forests are among the most threatened ecosystems at this moment and large areas have been converted rapidly into grass lands, secondary forest, savanna or agricultural land. Knowledge of seed germination and seedling establishment is required for the success of these forests and for a sustainable management of these forests. Fieldwork of this study was conducted in tropical dry forest INPA, eastern Bolivia, during a period of four months (November 2004 – February 2005). A spiny bromeliad (*Pseudananas sagenarius*) covers large areas in this forest and is believed to reduce tree regeneration of commercially important timber species. Seed predation was evaluated in areas containing three different bromeliad covers; high density (70-100% bromeliad), low density (0-30% bromeliad) and no cover (0% bromeliad). Seeds of two important timber species were artificially dispersed and the number of removed seeds was followed over 30 days. The time of discovering seeds by seed removers did not vary significantly among bromeliad densities, while removal rates during the experiment and removal percentages at the end of the experiment significantly differed between areas with and without bromeliad cover. Though, not the density, but only the presence of bromeliad seemed to have an effect on seed predation. Herbivory, survival and growth of seedlings were evaluated using four treatments consisted of the four possible combinations between bromeliad and exclosure. Herbivory, survival and growth of seven important timber seedling species were measured once in November 2004 and second in January 2005, but showed no significant affect on the treatments. Survival could not be tested on significance, but seemed to react on the treatments. Seedlings protected from herbivores showed no effect on bromeliad cover, while unprotected seedlings in areas with removed bromeliad showed a greater number of survivors. Herbivory of seedlings reduced seedling survival and absolute shoot growth. Measuring several microhabitat characteristics gave more insight in the distribution of bromeliad through the forest. Bromeliad densities are greater in the higher parts of the forest which contain less soil moisture contents and experience higher seed removal rates. At these sites, the ground cover with herbs, the number of seedlings and seedling species is lower. This study supports the hypothesis that seed predation reduces the number of available seeds for germination and with this tree regeneration. However, the presence of bromeliad did not show to have any effect on the herbivory, survival and growth of seedlings.

Introduction

Tropical dry forests occur over large areas in the world and have an important economic and ecological value. Once, these dry forests constituted about 40% of all forests in the tropics (Murphy & Lugo 1986), but now tropical dry forests are few, and perhaps they are the most threatened, less protected (Murphy & Lugo 1986, Gerhardt 1993) and least understood tropical forests in the world (Murphy & Lugo 1986). One of the largest remaining areas of tropical dry forest at the moment is represented by the dry forests of eastern Bolivia (Parker *et al.* 1993) and contains the most diverse dry forest in the Neotropics (Killeen *et al.* 1998). Nevertheless, this area has been identified as one of the most endangered ecosystems of South America, and these forests are today considered to be even more threatened than tropical rain forests (Gerhardt 1993). Due to recent industrial agriculture and urban expansion, tropical dry forests have been extensively converted into grasslands, open secondary forest, savanna, cattle ranches or agricultural land (Murphy & Lugo 1986, Reader 1987, Khurana & Singh 2001) and are approaching elimination. This conversion of tropical forests is a major threat to biodiversity, and therefore, dry forest ecosystems in the tropics have received a great attention by biologists in the last few years (Bullock *et al.* 1995, Jardim *et al.* 2003).

The problems in dry forests in eastern Bolivia mimic past events of deforestation and fragmentation in Argentina, Paraguay and Eastern Brazil (Killeen *et al.* 1998). Deforestation is a serious environmental problem, and managing forests for both timber production and species conservation should become increasingly important (Reader 1987, Killeen *et al.* 1998). In Bolivia the tropical dry forests have a great potential for timber forest management as an important source of income for both indigenous communities and industrial corporations (Mostacedo, *proposál*). However, a critical step towards sustainable forestry and tree regeneration is ensuring the establishment of seedling and sapling regeneration of commercially economic tree species (Mostacedo *et al.* 1998, Mostacedo & Fredericksen 1999), and it is imperative that silviculturists learn how to regenerate the valuable timber species (Fredericksen *et al.* 2000, Fredericksen & Mostacedo 2000). Therefore, knowledge of at least a part of the biota in a forest is required (Killeen *et al.* 1998), and studies of factors preventing or promoting seed predation and seedling establishment of commercially economic important timber species within tropical dry forests are necessary for understanding the regeneration dynamics of these forests (Mostacedo & Fredericksen 1999, Khurana & Singh 2001) which still are poorly investigated.

Background

Dry tropical forests occur in regions experiencing extended dry periods within the annual cycle and frequent severe droughts, which may have conditioned survival strategies of species populations (Khurana & Singh 2001). In these forests, regeneration of timber trees is not well understood and only a few studies have been carried out. In tropical dry forest of eastern Bolivia, approximately 20% of the 100 canopy tree species are used for timber exploitation. Most of these trees are dense-wooded species that are used for flooring and high quality furniture (Mostacedo, *proposál*). Tree regeneration is sufficient for only a few species, and of the 100 tree species Mostacedo studied in 815 m², only six timber species and five non-timber species had seedlings (Mostacedo, *proposál*). Spatial-temporal

variations within the tropical dry forest biome in soil moisture, light, nutrients, and intensity of competition and predation together regulate the seed germination, seedling establishment and survival (Gerhardt 1996 a&b, Khurana & Singh 2000 & 2001) and could possibly affect tree regeneration.

Mostacedo has during four years of his study in a tropical dry forest in eastern Bolivia observed that water availability and shade are the main factors that are limiting seedling recruitment (Mostacedo, *proposál*). Several other studies in tropical dry forests have found the same key factors, competition for moisture and light, which are influencing germination, growth and survival of plant communities (Lugo *et al.* 1978, Howe 1990, Rincón & Huante 1993, Gerhardt 1996a). The degree of deciduousness in dry forests is most probably related to water availability (Lieberman & Lieberman 1984, Reich & Borchert 1984), which is influenced by rainfall. Rainfall is highly seasonal and water availability can be a limiting factor for plant performance during the dry season (Poorter & Hayashida-Oliver 2000, Khurana & Singh 2001). Most seeds of dry tropical tree species mature in the dry season when the soil moisture content is very low and are dispersed at the beginning of the rainy season, when sufficient moisture is available for germination and seedling growth (Khurana & Singh 2001). Germination is triggered when water becomes available (Garwood 1983) and growth is limited to the rainy season (Rincón & Huante 1993, Gerhardt 1996 a&b). Apart from water, light availability is also a main factor affecting recruitment patterns. Among dry forest seedlings, differences have been found in germination, survival and seedling growth as response on light availability (Poorter & Hayashida-Oliver 2000, Khurana & Singh 2001). Garwood (1983) found that rainforest canopy trees are able to germinate in forest understorey, while Clark & Clark (1987) and Denslow (1987) found that seedling growth and survival are usually low in a rainforest. Howe (1990) related light availability to seedling development in a seasonal moist forest in Panama, and Rincón & Huante (1993) showed in their study in a Mexican deciduous dry forest increased growth rates with increasing light availability. Kennerd & Putz (2004) found this same positive relationship between growth and light availability. In a dry forest in Ghana, Lieberman & Li (1992) found higher seedling densities in well-shaded sites than in exposed, open sites. Shade appears to improve survival (Gerhardt 1996 a&b, Rose 2000). Higher light intensities could have contributed to higher defoliation levels in gap treatments, and this has a greater negative effect on seedling mortality (Gerhardt 1998). In the dry season seedlings generally experience high mortality, compared with the growing season when there is more rainfall (Gerhardt 1996b).

Within the annual cycle, most of the tree species are deciduous during the dry period (Fredericksen *et al.* 2000). Leaves fall on the ground and the thick leaf litter will lower the temperature and evaporation in the forest understorey (Gerhardt 1996a, Cintra 1997). A deep leaf litter may enhance seed germination and survival by decreasing variation in temperature and evaporation (Cintra 1997), but can also have a negative effect on seedlings. Due to a thick leaf layer light availability could be too low for seedling growth or seeds might not reach the soil and germinate. Fredericksen *et al.* (2000) and Cintra (1997) have found that in a high leaf litter cover small seeded species are easily hidden from seed predators than larger seeds, and due to this, predation on large seeds will be higher.

In studies of Wenny (2000) a very high degree of post-dispersal seed predation, which occurs once seeds have dispersed away from their parent, was found in study sites with dense vegetation

and cloudy conditions, providing small rodent protection from predators. Reader & Beisner (1991) found reduced seed numbers and seedling emergence of old-field forbs in Ontario when ground cover is dense and they found that the effect is species specific. Post-dispersal seed predation is largely carried out by larger organisms such as rodents, but ants are also important post-dispersal seed predators (Crawley 1992, Hulme 1998). In the Bolivian dry forest, large patches of terrestrial bromeliad (*Pseudananas sagenarius*) cover the ground. Because of its leaf and root morphology this species competes with tree seedlings for light and water (Brokaw 1983, Fredericksen & Mostacedo 2000). Bromeliad also capture seeds in their rosettes falling from the mother tree (Brokaw 1983). The bromeliad cover may account for the low densities and growth rates of commercial tree seedlings (Fredericksen & Mostacedo 2000), and suppresses the regeneration of trees and other plant species in the forest (Fredericksen *et al.* 1999). In addition, there is a possibility that the spiny bromeliad are used as a refuge by rodents that are the main seed predators and seedling herbivores in this forest. Terrestrial bromeliad are not only responsible for a low regeneration of plant and tree species in South America, also in Panama large terrestrial bromeliad colonies were found and causing the same problems (Brokaw 1983, Pfitsch & Smith 1988).

Besides the abiotic factors water, light, leaf litter thickness and ground cover, biotic factors such as seedling mortality and herbivory have an influence on the spatial pattern of seedling recruitment (Janzen 1970, Cintra & Horna 1997). Post-dispersal seed predation can also result in reduced seedling establishment, and this is as well a major constraint on tropical forest regeneration (Asquith *et al.* 1997). Seed losses to predators can be great, and it is not uncommon for plants to lose more than 80% of a given seed crop to seed predators (Schupp 1988, Crawley 1992, Hulme 1998). Herbivory damage has not only a great impact on tree regeneration, but also influences seedling survival and seedling growth. Herbivores themselves are also influenced by both biotic and abiotic factors, such as leaf age and quality, as well as plant size and light environment. They might influence herbivory rates and feeding behaviour (Gerhardt 1998). Coley & Aide (1991) concluded from their research that young leaves are the most favoured, and leaf toughness was related to herbivory rate (Coley 1983). Herbivory may be especially important in dry forests, since in these forests seasonality restricts plant growth (Reich & Borchert 1984). Seedling growth is limited to the rainy season (Rincón & Huante 1993, Gerhardt 1996 a&b) and the number of herbivores is highest during that season as well (Janzen 1981). Although studies have investigated “plant-herbivore interactions” (Howe 1990), the patterns of herbivory and seedling damage caused by habitat conditions have been relatively little explored.

The central hypothesis of this study is that there is a low rate of successful regeneration of commercially important timber species in the tropical dry forest INPA in the department of Santa Cruz, eastern Bolivia, because of the presence of a spiny terrestrial bromeliad (*Pseudananas sagenarius*). The study focuses on seed predation of two important timber species and on herbivory, survival and growth of seedlings of seven commercially important timber species in the dry forest INPA. In this area *P. sagenarius* covers large areas of the forest floor which may affect the rate of seed predation and may affect herbivory, survival and growth of seedlings by reducing water and light availability and creating a refuge for small seed predators and herbivores. Therefore, bromeliad cover might be a

possible reason for the limited tree regeneration in dry forests. The objective of this study is not only to determine the influence of bromeliad cover on the predation of seeds, and on herbivory, survival and growth of seedlings, but also to determine the influence of microhabitat characteristics on the distribution of *P. sagenarius* through the forest.

The hypothesis for the effect of bromeliad on seed predation is that areas with a high bromeliad cover provide more refuge for small seed predators and due to this the seed predation rate will be higher in areas with a high bromeliad cover compared to areas without bromeliad cover. For the effect of bromeliad cover on seedling herbivory, survival and growth could be hypothesized that bromeliad cover a positive effect has on seedling herbivory, but a negative effect on survival and growth. The spiny bromeliad provides an extraordinary refuge for herbivores against their own predators and due to this seedling herbivory will be higher with an increasing cover of bromeliad. Seedlings under a dense cover of bromeliad have a strong competition for water and light, and seedling growth and survival will be reduced. Seedling herbivory has also a negative impact on seedling survival and growth and with increasing herbivory rates, seedling survival and growth will be reduced. The distribution of bromeliad through the forest will be influenced by microhabitat characteristics. A hypothesis for this is that bromeliad colonizes large areas with medium to high light conditions, but not valleys or other sites with high soil moisture contents. Bromeliad is a good competitor for water due to its leaves which form rosettes and root system, and the number of bromeliads increases with increasing light availability. The reproduction of bromeliad can be vegetative and clonal.

Material and Methods

Study site

Studies were conducted at INPA Parket (16° 6' 45"S and 61° 42' 47"W), a 30.000 ha tract of privately-owned seasonally dry tropical forest in the Province of Ñuflo de Chávez in the Department of Santa Cruz, eastern Bolivia. INPA forest is located 30 km northeast of the town of Concepción and 250 km northeast of the city of Santa Cruz (Fig. 1). The specific study area had a topographic relief variation between 220 and 240 m (Instituto Boliviano de Investigación Forestal (IBIF), pers. comun, 2005). Seasonal mean temperature at Concepción is 24.3 °C with temperatures that vary between 3 °C in July and 38.1 °C in October (Killeen *et al.* 1990). The area receives an annual rainfall of 1129 mm, with a dry season (< 100 mm m⁻¹) from May to October (Killeen *et al.* 1990). The soils are reddish brown, sandy clay loams and most soil pits on the interfluves encounter bedrock within 70 cm of the soil surface (Navarro 1995). The natural vegetation is classified as tropical dry forest (Holdridge 1967) and the canopy stratum which is mostly deciduous during the 5-6 month dry season ranges from 20-25 m in height. This ecosystem contains high densities of commercially valuable species and several species are being commercial exploited, such as *Anadenanthera macrocarpa*, *Aspicosperma cylindrocarpon*, *Astronium urundeuva*, *Cariniana estrellensis*, *Centrolobium microchaete*, *Copaifera chodatiana*, *Cordia alliodora*, *Schinopsis brasiliensis* and *Tabebuia impetiginosa* (Killeen *et al.* 1998, Jardim *et al.* 2003). The general study area was a 160 ha management area exploited in 2000 using single tree selection on a diameter-limited basis (IBIF). A spiny ground bromeliad (*Pseudananas sagenarius*) is distributed over large areas of the forest floor in INPA (Fredericksen *et al.* 1999).

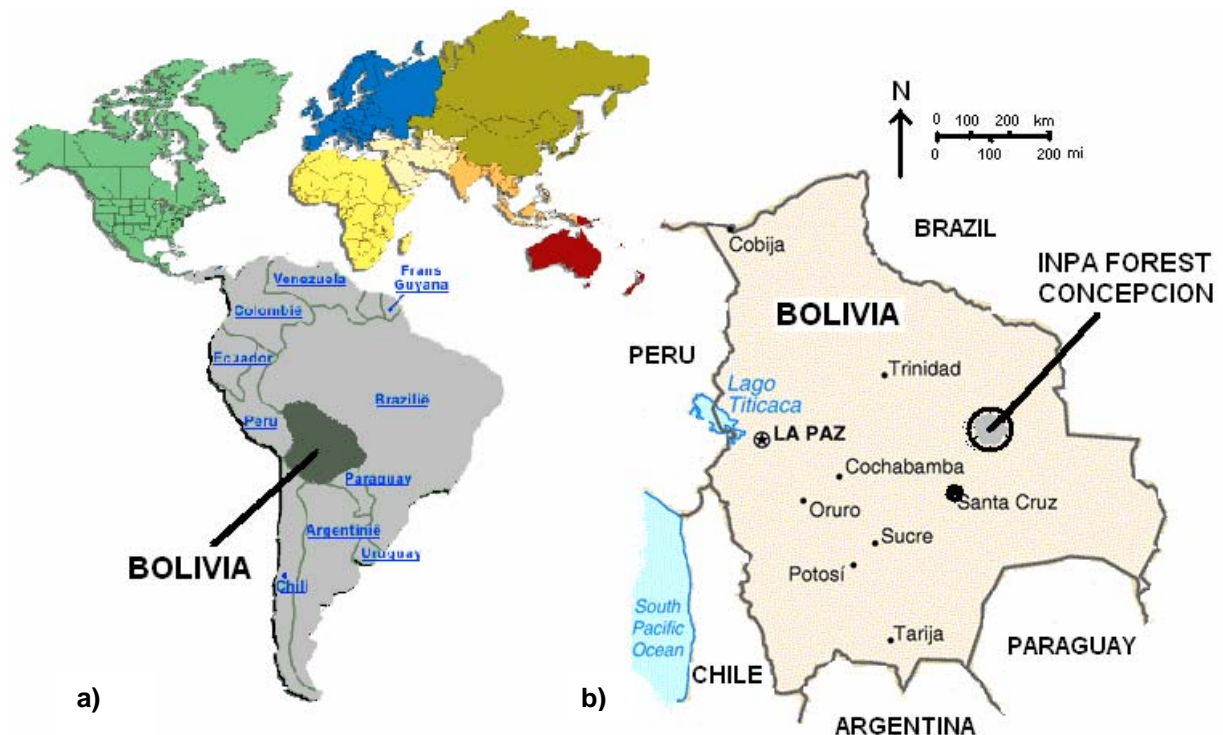


Fig. 1. Map of (a) the world with and an enlargement of South America in which Bolivia is located and a map of (b) Bolivia with the study area INPA parket, a dry forest located close to the town of Concepción in eastern Bolivia.

Study species

Seven commercially important timber species were chosen in this study to examine the relationship between bromeliad density and the rate of seed predation and seedling herbivory, survival and growth. The following timber species were included in the studies, named by their scientific name, family name between brackets and common name between quotation signs: *Schinopsis brasiliensis* (Anacardiaceae) "Soto", *Aspidosperma* sp. (Apocynaceae) "Jichituriqui", *Copaifera chodatiana* (Caesalpinaceae/Leguminosae) "Sirari", *Amburana cearensis* (Fabaceae/Leguminosae) "Roble", *Machaerium scleroxylum* (Fabaceae/Leguminosae) "Morado", *Acosmium cardenasii* (Fabaceae/Leguminosae) "Tasáa", and *Anadenanthera macrocarpa* (Mimosaceae/Leguminosae) "Curupaú". All of them occur naturally in the area, and differ in their life history strategy (Appendix 1). In the text species will be referred to only by generic name.

The terrestrial bromeliad *Pseudonanas sagenarius* (Bromeliaceae) is a spiny rosette forming understorey plant, locally known as "Gabaratá" (Fredericksen *et al.* 1999). *P. sagenarius* occurs in the tropical dry forests of eastern Bolivia, and is also distributed to Ecuador, Brazil, Paraguay and Argentina. It is an important ecological factor because it is an abundant species, it is clonal and often forms dense, nearly monospecific stands which cover large areas of the forest floor (Fredericksen *et al.* 1999). *P. sagenarius* also has a rapid vegetative reproduction and forms fruits which are important for the fauna. The fast reproduction and great abundance of this bromeliad inhibits the establishment of other plants in the forest (Fredericksen *et al.* 1999). Hereafter, *Pseudonanas sagenarius* will be referred to as bromeliad.

Study design

Experimental and observational data were collected from November 2004 to February 2005 in separated parts of the forest to test the assumption that bromeliad cover has an effect on seed predation and on seedling herbivory, growth and survival, and to determine the distribution of bromeliad through the forest.

To study the effect of bromeliad cover on seed predation, a seed predation experiment was set up in which seeds of two species, *C. chodatiana* and *M. scleroxylum*, were exposed to different bromeliad densities. The study area was restricted to a 20 ha section harvested in 2000. In December 2004 seventy-nine plots of 2x2 m were selected with three naturally occurring bromeliad densities: (1) high bromeliad density (70-100%), (2) low bromeliad density (0-30%), and (3) no bromeliad density (0%) (Table 1). Plots were at least 50 m apart. In January 2005 a seed depot was placed in the middle of each plot. Ten seeds of *C. chodatiana* or *M. scleroxylum* were put in each of these 79 depots and were exposed to seed predators during 30 days. A total of 390 *M. scleroxylum* and 400 *C. chodatiana* seeds were used, which were collected from trees located at the study site during April-June 2004 (*M. scleroxylum* seeds during June 2004 and *C. chodatiana* seeds during April-May 2004). After seed collection, seeds were dried in the sun. Seeds damaged by predators, fungi or by other causes were visually detected and excluded, and only viable seeds were used in the experiment.

Table 1. Number of seed depots for each of the three bromeliad densities separated for the two seed species, the total number of seed depots per species and per bromeliad density, and the complete number of seed depots used in the seed predation experiment.

Bromeliad density Species	High bromeliad density	Low bromeliad density	No bromeliad density	Number of seed depots per species
<i>Machaerium scleroxylum</i>	14	12	13	39
<i>Copaifera chodatiana</i>	14	13	13	40
Number of seed depots per bromeliad density	28	25	26	79

As a way to document the effect of bromeliad cover and the impact of herbivores on seedling herbivory, growth and survival, four treatments were set up and each treatment was replicated ten times. In total forty plots were selected in September 2004, and in most of these plots bromeliad ground cover occurred. In total twenty plots were needed without bromeliad, and therefore some of the selected plots in which bromeliad occurred had to be cleared by removing only the bromeliad cover in an area of approximately 4 m². In ten of each of the twenty plots with and without bromeliad, exclosures of 1x1 m were placed to exclude mammals and other herbivores. In this way four different treatments were created (Table 2). In each of the forty experimental plots seeds were sown in seven rows in September 2004. The order of the rows was chosen at random and each row counted ten seeds of the same species. In November 2004 seeds of the seven species in all forty plots had germinated and started growing. At the end of November 2004 measurements of herbivory and initial stem length were made. A second measurement was made after two months at the end of January 2005.

Table 2. Design for all experimental plots used in the seedling regeneration study with a combination of bromeliad and exclosures (+ means present; -- means absent), the total number of plots used for each of the four treatments and the total number of plots used in the regeneration study.

Treatment	Bromeliad	Exclosure	Number of plots per treatment
1	++	++	10
2	++	--	10
3	--	++	10
4	--	--	10
Total number of experimental plots			40

Microhabitat characteristics were measured to determine which environmental variables are important for the establishment of *P. sagenarius*, and to determine the effect of the surrounding environment on seed predation and tree regeneration of commercially important tree species.

Seed predation experiment

In each of the 79 plots of 4 m² a self constructed seed depot was placed in the centre to evaluate seed predation. The depots had a triangular shape (25 cm per side) and were made of grey coloured iron mosquito netting with a mesh size of 2.5 mm. The edges of the triangle were folded upright to allow rainwater drainage and prevent the seeds from being washed away and because of the thickness of the leaf litter layer at the moment, which makes it very hard to find the seeds back. Seed depots were attached to the ground at each corner by metal stalks made of approximately 10 cm long pieces of iron wire. After being attached to the ground, the edges outside the depots were covered with leaves in order to mimic the natural situation as closely as possible.

In January 2005 at each of the 79 plots ten seeds of one species were added to the seed depot at a given bromeliad density, to assess the rate of seed predation. The seeds were set out complete with whatever protective tissues would normally accompany them after natural seed dispersal. Seed depots were checked on day 1, 2, 4, 8, 14 and 30 after seed placement. After these 30 days the effect of seed predators had to be determined, because at this time there is a high possibility that seeds have germinated. At each evaluation day the number of intact seeds remaining in the seed depots was recorded as the number of survived seeds. Seeds were considered to have been removed if they were found outside the seed depot or had completely disappeared. Seeds in the depot which were damaged, partly eaten or infested to such an extent that it seemed unlikely to the observer that the seed could survive and germinate, were removed from the seed depots by the observer and also mentioned as removed seeds. It is important to note that seed removal has been measured, not seed predation, because the final fate of each seed after being removed from the seed depot is unknown. Each day of checking the seed depots, litter falling into the depots was removed and the same walking paths were used to check the depots, to reduce damage to the surrounding vegetation. Once seeds are dispersed, they are likely to be removed by ants or small mammals.

According to de Boo (2001) and Peña-Claros & de Boo (2002), seed depots did not have a positive or negative influence on the foraging behaviour of animals. In their studies, seeds placed directly on the forest floor showed the same removal rate as seeds placed in the seed depots.

The average time in days of discovering a seed depot is the number of days until the first visit of a seed predator to a seed depot averaged per seed species of all seed depots with the same bromeliad density and of all seed depots pooled together. One-way analysis of variance (ANOVA) was used to determine if there were significant differences between and within species. To determine if microhabitat characteristics, such as soil moisture content, canopy cover, crown position, leaf litter thickness, different ground cover types, basal area, tree density and geographic altitude, had an effect on the time needed to discover a seed depot, single linear regressions were performed.

Seed removal data were analysed with a survival analysis. A Cox regression was used to evaluate the effect of bromeliad density on the removal of seeds through time. For the analysis the day of census was used in which the seed depots were visited by observers to check on removed seeds. Seed depots were pooled per species and per bromeliad density. Simple contrasts were carried out

with the bromeliad density as a categorical covariate to find significant differences in seed removal among the three bromeliad densities high, low and no.

To evaluate the effect of environmental variables on seed removal, the seed removal rate or slope was calculated for each individual seed depot by regressing the number of removed seeds against the time. The removal rates obtained per seed depot were then regressed against each microhabitat characteristic separately, using linear regression analysis. An environmental variable was used as the independent variable and the removal rate was used as the dependent variable. These analyses were performed per species. Microhabitat characteristics were correlated to each other using Pearson correlations, by pooling data of all treatments and all species together. The differences between the three bromeliad covers among the microhabitat characteristics were analysed using a one-way ANOVA. A Student-Newman-Keuls test was used as a Post-Hoc test. Data on the cover of herbs and woody species in percentages had unequal variances according to Levene's Statistics, and therefore non-parametric Kruskal-Wallis tests were used with the three bromeliad classes as factor.

All statistical analyses were carried out using SPSS (12.0 edition, 2004) and a comparison was considered as significant only when *P*-value of comparisons was < 0.05.

Seedling regeneration experiment

In the study area close to the field station, five different transects were chosen and in each transect two replicates of the four different treatments were at random installed. In total there were forty plots of 1 m² and each treatment was replicated ten times. Exclosures were constructed in September 2004 from wooden stakes, grey coloured iron mosquito netting with a mesh size of 2.5 mm and thick plastic. Four wooden stakes were pounded into the ground in the corners of a 1x1 m square and the tops of the wooden stakes were approximately 2.0 m above the ground. From the ground mosquito netting was put around the wooden stakes for the first 0.4 m, and above this the wooden stakes were surrounded for another meter by thick transparent plastic. The bottom edges of the mosquito netting were buried 5 cm below ground to prevent passage of small mammals underneath. The tops of the exclosures were open to allow normal accumulation of fallen debris, known to be an important mortality agent (Clark & Clark 1987). Although small rodents can probably climb such exclosures and insects might climb or fly into the exclosures, herbivory by medium and large-sized mammals is expected to be minimized. The most common insect predators are leaf cutter ants (M. Grol, *personal observations*, 2004-2005).

Herbivory rate, survival and growth were measured twice of the seven seedling species which had germinated within the forty experimental plots, first the end of November 2004 and second the end of January 2005, to determine differences between species and the four treatments. In November 2004 in all plots the three most intact leaves of each seedling were selected and marked with different coloured straws around the twig. In some plots seedlings of *Aspidosperma* sp., *C. chodatiana* and *A. cearensis* were abundant in November 2004, therefore a maximum of three randomly selected individuals per row in each plot were selected for the herbivory experiment, while seedling height was measured of all present seedlings. For each marked leaf separately, the total leaf area and damaged

leaf area were quantified by placing a clear plastic grid sheet (4 squares/cm²) over the leaf and counting squares. Marked seedlings were resurveyed once more after two months in January 2005, in order to evaluate the percentage of herbivory, growth and survival of seedlings in the four different treatments. Seedlings have been variously defined as individuals still dependent on seed reserves for growth (Garwood 1983). In practice it is difficult to establish whether plants still depend on their seed reserves. Therefore seedlings in this study are defined as plants with a height up to 2 m.

A. macrocarpa has bipinnate leaves and for this species it was impossible to count grid squares. Therefore, not the number of squares was used to evaluate herbivory, but the visually estimated percentage of herbivory was used. Species of *S.brasiliensis*, *Aspidosperma* sp., *C. chodatiana*, *M. scleroxylum* and *A. cardenasii* did not have fully expanded leaves in November 2004 and January 2005 and for that reason the percentage of herbivory was measured of the cotyledons. Seedlings with some missing leaves at the second measurement were considered to be survivors, while the missing leaves were considered to be eaten. Other types of leaf damage were partly eaten leaves, holes, mines, galls, and scraped leaf surfaces caused by herbivorous mammals and insects. These damages were measured and used in the calculations for herbivory. Plants were recorded as dead when the stem was dry or when the marked seedling was missing. These seedlings did not survive and had suffered 100% herbivory. The difference between the number of grids at the first and the second measurement is an indication for the herbivory pressure.

The predation rate per leaf in percentages was calculated separately for November 2004 and January 2005 by dividing the number of damaged grids per leaf by the total number of grids per leaf times 100%. The percentage of herbivory per plant per month was calculated as:

$$\text{Herbivory} = \sum \frac{(\text{predation rate } t_2 - \text{predation rate } t_1)}{t_2 - t_1} * 30.5 \quad (\% / \text{month})$$

where t_1 and t_2 are the two measurement dates.

Seedling height was measured as the height of the main shoot for all germinated seedling species within the plot. Height increment was used as an index of growth and was calculated from differences in seedling height between the two measurements. Absolute shoot growth was used in this study instead of the relative growth rate (RGR) because only 1.9% of the variance was explained by the initial height of the seedlings (RGR; $R^2 = 0.019$). Absolute shoot growth in centimetres per plant per month was calculated as:

$$\text{Absolute shoot growth} = \frac{\text{height } t_2 - \text{height } t_1}{t_2 - t_1} * 30.5 \quad (\text{cm} / \text{month})$$

where t_1 and t_2 are the two measurement dates.

Analyses on herbivory were carried out using the data of the seven seedling species, but to make correct comparisons on the absolute shoot growth, species of *M. scleroxylum* and *S. brasiliensis* were excluded from the data analysis for absolute shoot growth. The number of shoot growth measurements of these two species was too low to use in the analysis, respectively four and one growth measurements.

Differences in herbivory and absolute shoot growth between species and treatments were performed using analyses of variance (ANOVA). Three-way ANOVAs were carried out to find significant effects of bromeliad, exclosure and species on herbivory and absolute shoot growth, with herbivory or absolute shoot growth as dependent variable and bromeliad, exclosure and species as main factors. Data on absolute shoot growth did not show unequal variances according to Levene's Statistics, but data on herbivory did. Therefore a Student-Newman-Keuls test was used as a Post-Hoc test to analyze the differences between species on absolute shoot growth, while a Dunnett's T3 test was used as a Post-Hoc test to analyze the differences between species on herbivory. Analysing which species had a reaction in absolute shoot growth as a result of the different treatments, two-way ANOVAs were computed, with herbivory as dependent variable, and bromeliad and exclosure as factors.

Chi-square Crosstabs with bromeliad, exclosure and survival at once could not be computed. Therefore Chi-square tests were computed for only two variables at the time per species and pooled for all species together. Crosstabs were made for survival * bromeliad and for survival * exclosure.

Linear regression analyses were carried out between habitat characteristics and herbivory, survival and shoot growth to investigate if there are relationships among all factors. One-way ANOVAs were performed to find an effect of herbivory on seedling growth and survival.

All statistical analyses were performed using SPSS (12.0 edition, 2004) and a comparison was mentioned as significant only when $P < 0.05$.

Microhabitat characteristics

To determine the relation of microhabitat characteristics on the distribution of bromeliad through the forest and on seed predation, different microhabitat characteristics of the 79 plots used for the seed predation experiment were measured. Some habitat characteristics were also measured in the forty plots of the seedling regeneration experiment to get more insight in the effect of the environment on seedling herbivory, growth and survival.

Germination is triggered and growth is stimulated when water becomes available (Lugo *et al.* 1978, Garwood 1983, Morris *et al.* 2000). Mortality is highest during the dry periods (Lieberman & Li 1992), and local soil conditions can be highly variable between areas. Therefore soil samples at a depth of 0-5 cm were collected in November 2004 in each of the 79 plots of the seed predation experiment and in November 2004 and January 2005 in each of the forty plots of the seedling regeneration experiment. Fresh soil weight was estimated directly after taking a soil sample and dry soil weight was estimated after oven-drying the soil at 65 °C for 72 hours. Soil moisture content as a percentage was calculated as:

$$\text{Soil moisture content} = \frac{\text{fresh soil weight (g)} - \text{dry soil weight (g)}}{\text{dry soil weight (g)}} * 100\% \quad (\%)$$

Canopy cover (light availability) is also known to be an important factor for germination, survival and tropical seedling growth (Howe 1990, Poorter & Hayashida-Oliver 2000, Khurana & Singh 2001, Kennard & Putz 2004). Therefore, light conditions were measured once in November 2004 in the four wind directions with a spherical densitometer (Forest Densimeters Inc., Bartlesville) in each plot for all studies. Canopy cover from these data can be calculated as:

$$\text{Canopy cover} = \frac{\sum \text{canopy cover four wind directions}}{4} * 1.04 \quad (\%)$$

Average canopy cover of the seed predation study was $95 \pm 3\%$ (mean \pm SD) and of the seedling regeneration study was $93 \pm 4\%$.

Using the Dawkins index modified by Clark & Clark (1987), two observers estimated visually the crown position to evaluate the amount of light that enters the ground (Table 3). Afterwards, the two measurements were averaged.

Table 3. Criteria of the Dawkins index modified by Clark & Clark (1987) used to evaluate the amount of light that enters the canopy stratum and reaches the ground.

Index	Description	
5	Emergent	Completely exposed crown to a 90° inverted cone of overhead light. Vertical and laterally light enters the plot.
4	Total vertical illumination	Full overhead light, at least 90% of the crown with direct incident light. Part of the vertically light entering the plot is intercepted by an adjacent crown.
3	Partial vertical illumination	Some overhead light, 10-90% of the crown lit from above. The plot is partially exposed to the vertical light and partly shaded by other crowns
Crown lit from the side and <10% of the total vertical projection enters the plot		
2.5	High lateral illumination	
2	Medium lateral illumination	
1.5	Low lateral illumination	
1	Without direct illumination	No direct light either from above or the side

The diameter of trees in centimetres was measured at a height of 1.3 m from the ground, diameter breast height (DBH). According to Mostacedo & Fredericksen (2001) DBH must be measured in an area of at least 25 m^2 , therefore trees $> 10 \text{ cm}$ in DBH were measured in a radius of 5 m from the centre of each plot in all studies in November 2004. From the DBH measurements, basal area and the density for each plot were calculated as:

$$\text{Basal area per tree} = \frac{1}{4} * \pi * (\text{DBH} / 100)^2 \quad (\text{m}^2)$$

$$\text{Basal area per plot} = \frac{\sum_1^N \frac{1}{4} * \pi * (\text{DBH} / 100)^2}{\pi * r^2} * 10000 \quad (\text{m}^2 / \text{ha})$$

$$\text{Density} = \frac{\text{number of DBH measurements in each plot}}{\pi * r^2} * 10000 \quad (\text{ha})$$

in which $\pi = 3.141592654$ and $r = 5$ m (Mostacedo & Fredericksen 2001). The maximum height in meters of the tree with the highest canopy above the plot is visually measured by two observers and averaged.

Geographic data of almost all seed predation plots in the study area were available by IBIF. Data of altitude were used to determine the effect of these factors on the distribution of bromeliad in the forest.

Leaf litter may influence seed predation and/or germination (Schupp 1988, Cintra 1997), and for this reason leaf litter depth and leaf litter cover were estimated in November 2004 for each plot of the seed predation study. Leaf litter depth in centimetres was estimated in each of the four corners of all sampling areas in the seed predation experiment, and averaged and leaf litter cover was estimated visually in percentages.

Vegetation densities may be related to rodent activity and seed predation. According to Mostacedo & Fredericksen (2001) estimations of vegetation density must be made in plots of at least 1 m^2 for herbs and seedlings, and in plots of at least 4 m^2 for lianas and woody species. Therefore the vegetation cover was estimated for the complete plots (4 m^2) in the seed predation study. Estimations in percentages of all ground vegetation cover < 2 m tall were visually made independently by two observers and averaged, and with the help of field assistants, plant and seedling identification was conducted. Separate measurements were made for the percentage of bromeliad, herbs, liana and woody species. Bromeliad densities might have an effect on the total number of seedlings and the total number of seedling species, and therefore they were counted in each site of the seed predation study for canopy tree species up to 2 meter tall. In the seed predation plots, bromeliad occurred in three classes; no, low and high density. In each plot where bromeliad existed, the number of bromeliad was counted and of each bromeliad the height was measured. Mean bromeliad height in centimetres was calculated by averaging all bromeliad heights within a plot.

Results

Bromeliad cover and environmental variables

The distribution of bromeliad through the forest was only significantly related to the microhabitat characteristics altitude, ground cover with herbs and the mean bromeliad height (Fig. 2), all other environmental variables did not show significant relations with the bromeliad density using one-way ANOVAs. The bromeliad cover was positively related to the altitude in meters, and therefore the bromeliad density increased as the altitude increased in a range of 320 to 343 metres (Fig. 2a). A significant difference was found between plots with a high bromeliad density and plots without bromeliad (ANOVA, $df = 2$, $F = 3,533$, $P = 0,035$), but plots with a low bromeliad density showed no significant difference with plots containing a high or no bromeliad density.

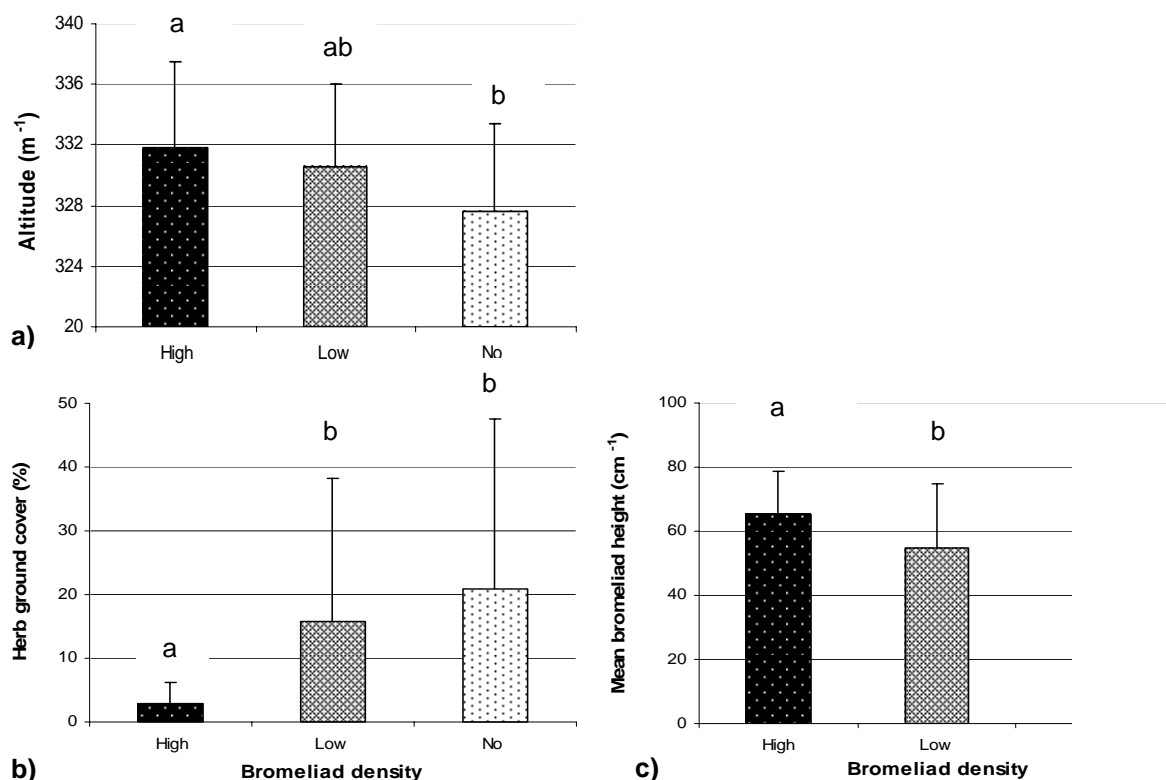


Fig. 2. Effect of microhabitat characteristics on the distribution of bromeliad through the forest, by pooling all plots within the same bromeliad category (+SD). A one-way ANOVA was used for (a) altitude in meters, and non-parametric Kruskal Wallis tests were used for (b) percentage ground cover with herbs and (c) mean height of the bromeliad in centimetres. Means with the same letter (a, b or c) within a graph are not significantly different ($P > 0.050$). High = 70-100%, low = 0-30% and no = 0% bromeliad.

The effect of ground cover with herbs on the different bromeliad densities showed unequal variances and a Kruskal Wallis test was used instead of an one-way ANOVA. Ground cover with herbs had a negative effect on the bromeliad density, and with an increasing percentage of herb ground cover the bromeliad density decreased (Fig. 2b). The bromeliad density showed to have a significant effect on the ground cover with herbs (Kruskal Wallis, $df = 2$, Chi-square = 12,132, $P = 0,002$). Between a high and a low bromeliad density and between a high and no bromeliad density significant

differences were found for the ground cover with herbs, but no significance was found between a low and no bromeliad density. For the mean bromeliad height, a significant difference was found between plots with a high bromeliad density and plots with a low bromeliad density (ANOVA, $df = 2$, $F = 5,275$, $P = 0,026$). Plots without bromeliad density did not contain bromeliad and could for this reason not be tested. Plots with a high bromeliad density showed to have the highest mean bromeliad height (Fig. 2c). Plots without bromeliad did not show a mean bromeliad height. The bromeliad density increased with an increasing altitude, but decreased with an increasing ground cover of herbs and with an increasing bromeliad density the mean bromeliad height increased as well.

Pearson correlations were performed between the microhabitat characteristics of all plots of the seed predation experiment and did show correlations between some environmental variables (Table 4). Significant correlations were found between altitude and percentage herb cover, mean bromeliad height, number of seedlings, number of seedling species and soil moisture content. More significant correlations were found between the liana ground cover and canopy cover and between the ground cover with woody species and the mean bromeliad height. Correlations were significant when the P-value was $< 0,050$.

Table 4. Relationships between microhabitat characteristics using Pearson correlations. The Pearson correlation coefficient, the R^2 values and the significance (P) are given for the correlations between different environmental variables. Correlations were mentioned as significant when the P-value was $< 0,050$.

Correlations between microhabitat characteristics		Pearson correlation	P
Altitude	Herb ground cover	-0,345	0,003
Altitude	Mean bromeliad height	0,277	0,019
Altitude	Number of seedlings	-0,247	0,036
Altitude	Number of seedling species	-0,342	0,003
Altitude	Soil moisture content	-0,479	0,000
Liana ground cover	Canopy cover	-0,260	0,021
Woody species cover	Mean bromeliad height	-0,358	0,001

The effect of bromeliad cover on the number of seedlings and the number of seedling species within a plot of the seed predation experiment was tested using one-way ANOVAs. The different bromeliad densities did not show any significant effect on the mean number of seedlings (ANOVA, $df = 2$, $F = 0,488$, $P = 0,616$), and the mean number of seedling species (ANOVA, $df = 2$, $F = 1,324$, $P = 0,272$).

Seed predation

There is a large difference in time that seed removers need to discover a seed depot (Fig. 3). Depots with seeds of *M. scleroxylum* pooled for all three bromeliad densities take much more time to be discovered than depots with seeds of *C. chodatiana* (13.7 ± 10.3 versus 2.7 ± 3.1 days). This difference between *M. scleroxylum* and *C. chodatiana* seeds can also be seen for each of the different bromeliad densities separate. The average time of the first visit to a depot with seeds of *M. scleroxylum* varied between the bromeliad densities. It took more time to discover a seed depot in the

high bromeliad density plots (16.43 ± 11.0 days) than in the plots with less bromeliad, and seeds in plots with low bromeliad densities were first discovered (10.8 ± 9.8 days). However, these differences were not significant (ANOVA, $df = 2$, $F = 1,218$, $P = 0,308$). Differences in discovering time between bromeliad densities for seeds of *C. chodatiana* were very small and also not significant (ANOVA, $df = 2$, $F = 0,188$, $P = 0,830$). Looking at seed discovering within the same bromeliad density between the two species, significant differences were found for each bromeliad density separately (ANOVA, $df = 1$, $P < 0.050$ for a high, low and no bromeliad density between species). No relations were found between the time needed to discover seed depots and any of the environmental characteristics using linear regressions.

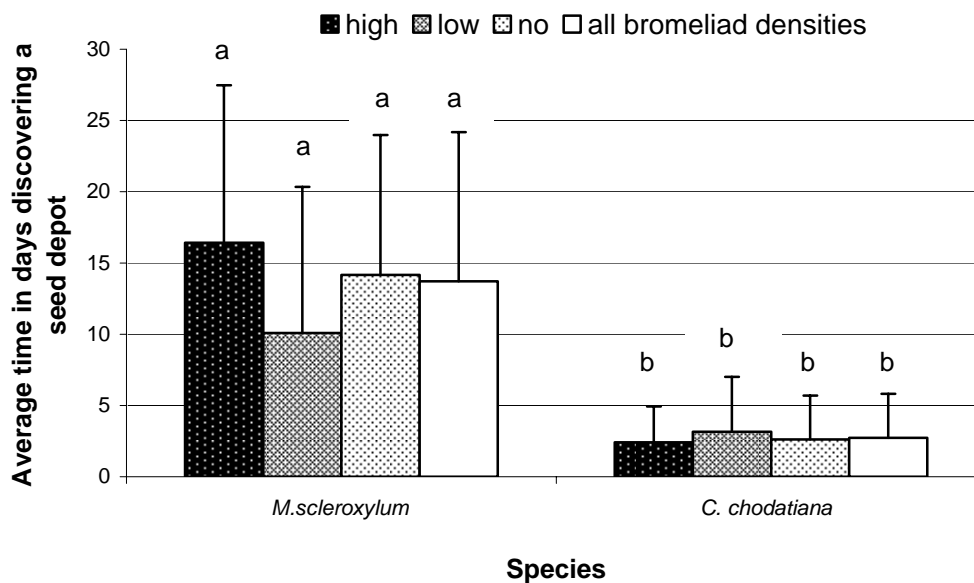


Fig. 3. The average time in days in which a plot was discovered for the first time by a seed predator for each seed species at a specific bromeliad density (+SD) and the average time of discovering a seed depot per seed species pooled for all three bromeliad densities (+SD). Columns with different letters (a or b) are significantly different ($P < 0,050$). High = 70-100% bromeliad density, low = 0-30% bromeliad density, no = 0% bromeliad, and all bromeliad densities are all densities pooled together.

Using a Cox regression (Table 5a, Fig. 4), significant differences were found in the removal of seeds during 30 days between low bromeliad densities and no bromeliad for each species separated (Cox regression, $df = 1$, $P = 0,032$ and $P = 0,016$ for respectively *M. scleroxylum* and *C. chodatiana*). Significant differences in removal rate between plots with a high bromeliad density and plots without bromeliad were found for seeds of *C. chodatiana* (Cox regression, $df = 1$, $P = 0,006$), while for *M. scleroxylum* seeds the removal rate did not vary significantly between plots with a high bromeliad density and plots without bromeliad during 30 days. Between high and low bromeliad densities also no significant differences were found for each species separately.

The total percentage of removed seeds after 30 days varied between the two species from 43% for *M. scleroxylum* to 95% for *C. chodatiana*, and between the three bromeliad densities from 64% for no bromeliad density to 76% for a low bromeliad density (Table 5b). For both species the highest removal percentages after 30 days were found in plots with a low bromeliad density (52.5 and 96.9 %

for respectively *M. scleroxylum* and *C. chodatiana*), and the lowest removal percentages were found in plots without bromeliad (34.6 and 93.1 % for respectively *M. scleroxylum* and *C. chodatiana*) (Table 5).

Table 5. (a) Results of the Cox regression analysis testing for the effect of bromeliad density on the removal rate of *M. scleroxylum* and *C. chodatiana* seeds during 30 days. Bromeliad densities in a given row followed by the same letter (a or b) are not significantly different ($P > 0,050$). (b) Removal percentages at the last day of the experiment (day 30) per species at a specific bromeliad density, per species pooled for all three bromeliad densities and per bromeliad density pooled for both species. High = 70-100% bromeliad, low = 0-30% bromeliad and no bromeliad density = 0% bromeliad in an experimental plot.

a)		Bromeliad density		
Seed species	High	Low	No	
<i>Machaerium scleroxylum</i>	ab	a	b	
<i>Copaifera chodatiana</i>	a	a	b	

b)		Bromeliad density			Total removal percentage per species
Seed species	High	Low	No		
<i>Machaerium scleroxylum</i>	42,9	52,5	34,6	43,1	
<i>Copaifera chodatiana</i>	95	96,9	93,1	95,0	
Total removal percentage per bromeliad density	68,9	75,6	63,8		

At day 0 the proportion of remaining seeds was 1.0 for both seed species (Fig. 4). Seeds of *M. scleroxylum* were removed slower and without large differences in removal rates between the three bromeliad densities, while seeds of *C. chodatiana* were removed much faster, especially in plots in which bromeliad is present.

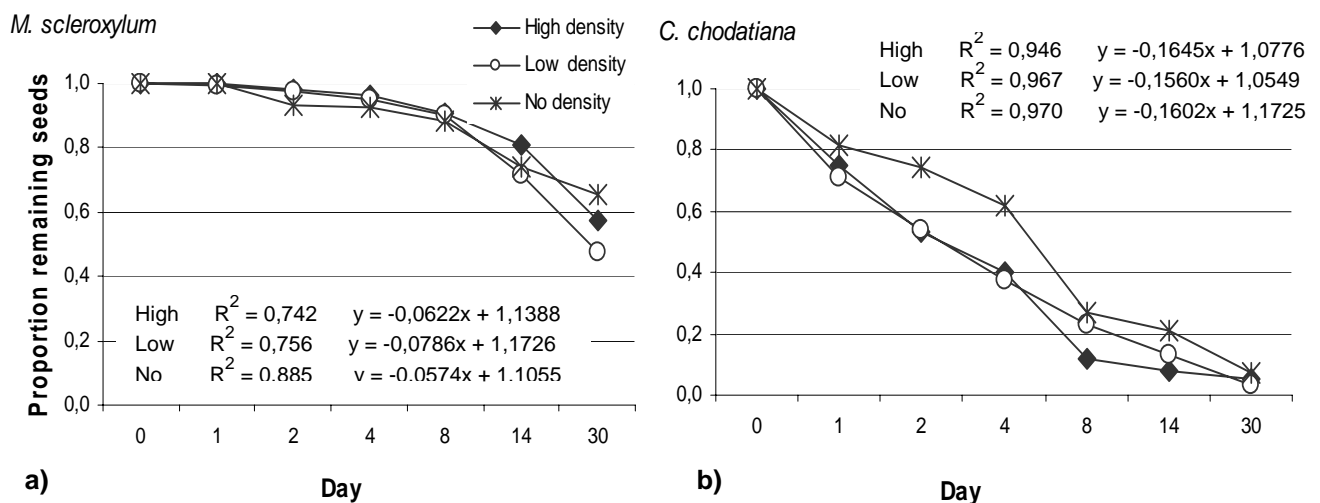


Fig. 4. Proportion of remaining seeds over a period of 30 days for (a) *M. scleroxylum* and (b) *C. chodatiana* seeds for each bromeliad density separately. Data represented are mean of all plots pooled per bromeliad density at day 0, 1, 2, 4, 8, 14 and 30. R squares are given of the regression lines for each bromeliad density per species. High density = 70-100%, low density = 0-30% and no density = 0% bromeliad.

After 30 days almost half of the in total 390 *M. scleroxylum* seeds were removed (43%), and the proportion of remaining seeds was 0,571 for a high bromeliad density, 0,475 for a low bromeliad density and 0,654 for no bromeliad density (Fig. 4a). Half of the in total 400 *C. chodatiana* seeds were removed after 2 days in plots with a high and low bromeliad density (proportion remaining seeds is respectively 0,536 and 0,538) and after approximately 6 days in plots without bromeliad. After 30 days only a small proportion of *C. chodatiana* seeds remained in total (5%), and the proportion of remaining seeds after 30 days was 0,050 for a high bromeliad density, 0,031 for a low bromeliad density and 0,069 for no bromeliad density (Fig. 4b).

The seed removal rate or slope of *M. scleroxylum* seeds could not be explained by one of the microhabitat characteristics using linear regressions ($P > 0,050$), while the seed removal rate of *C. chodatiana* could partially be explained by the characteristics altitude and canopy cover (Fig. 5). The removal rate of *C. chodatiana* was positively related to altitude (linear regression, $P = 0,005$) (Fig. 5a) and negatively related to canopy cover (linear regression, $P = 0,020$) (Fig. 5b). The removal rate increased as the altitude of the plots increased or as the canopy cover decreased.

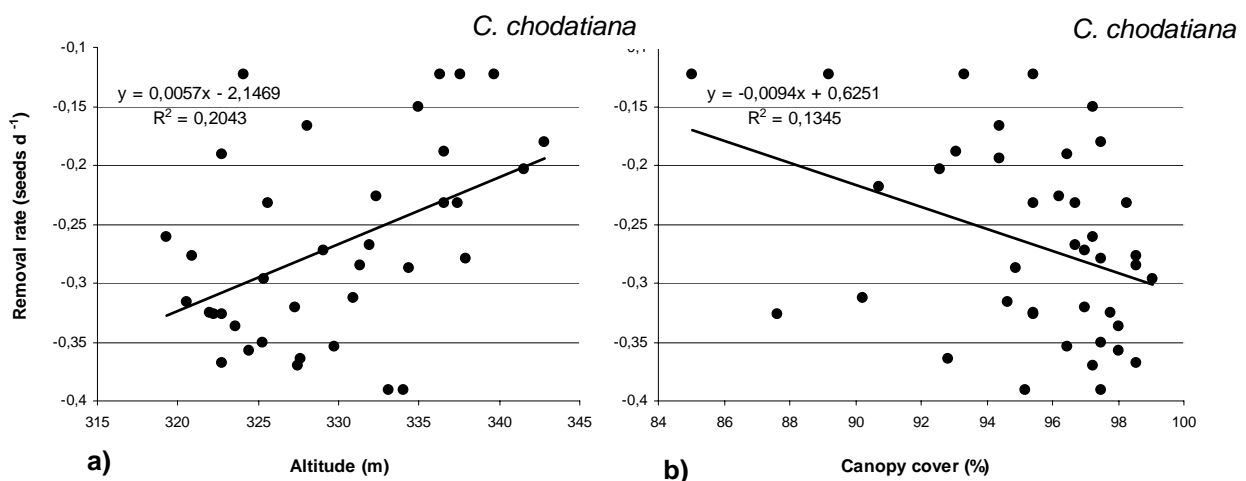


Fig. 5. The relationship between the removal rate of *C. chodatiana* seeds and microhabitat characteristics using linear regressions. (a) The positive relationship between removal rate and altitude in meters and (b) the negative relationship between removal rate and canopy cover in percentages.

Seedling regeneration

Performing a three-way analysis of variance (ANOVA) for herbivory and absolute shoot growth separately among bromeliad, exclosure and species, some significant differences were found (Table 6). For the species *M. scleroxylum* and *S. brasiliensis* not enough data on absolute shoot growth were available in the present study and therefore they were excluded from the analysis. Bromeliad cover only, and not taking exclosures into account, did not influence the herbivory or absolute shoot growth pooled for all species, as well as the influence of only exclosures pooled for all species, and not taking the presence or absence of bromeliad into account (Table 6). However, exclosures did have an almost significant effect on the absolute shoot growth pooled for all species (ANOVA, $df = 1$, $F = 3,885$, $P = 0,053$). Statistics showed a significant difference in herbivory and absolute shoot growth between

species pooling data of all treatments together (ANOVA, df = 6, F = 7,624, P = 0,000 for herbivory and ANOVA, df = 4, F = 3,561, P = 0,011 for absolute shoot growth) (Table 6, Fig. 7). Bromeliad and exclosures combined did not have any influence on the percentage of herbivory or the absolute shoot growth pooled for all species and showed no significance (Table 6), while significant differences between species in the four treatments were found for absolute shoot growth (ANOVA, df = 4, F = 3,135, P = 0,020), but not for herbivory damage (Table 6).

Table 6. Three-way analysis of variance for (a) herbivory damage in percentages and (b) absolute shoot growth in centimetres among species, bromeliad and exclosures (brom = bromeliad and excl = exclosure). Data on herbivory and absolute shoot growth were pooled together separately for all plots with the same treatment and for all species together. Data on absolute shoot growth of *M. scleroxylum* and *S. brasiliensis* were excluded from the analysis. Differences were significant when the P-value was < 0,050.

	a) Herbivory				b) Absolute shoot growth			
	df	Type III SS	F	P	df	Type III SS	F	P
brom	1	102,36	0,494	0,483	1	0,31	2,311	0,133
excl	1	149,09	0,720	0,398	1	0,52	3,885	0,053
species	6	9475,51	7,624	0,000	4	1,89	3,561	0,011
brom * excl	1	460,79	2,225	0,138	1	0,23	1,717	0,195
brom * species	6	751,93	0,605	0,726	4	0,68	1,271	0,290
excl * species	6	2046,48	1,647	0,140	4	0,46	0,863	0,491
brom * excl * species	5	735,68	0,710	0,617	4	1,67	3,135	0,020
Error	119	24648,92			66	8,77		

Treatments with bromeliad and exclosures did not affect herbivory, only absolute shoot growth of only one species, *A. macrocarpa*. Seedlings of *A. macrocarpa* in plots without exclosures and covered with bromeliad did have the highest absolute shoot growth in contrast to the other treatments ($1,50 \pm 0,03$ cm) (Fig. 6). Seedlings in all other treatments did have a much lower mean absolute shoot growth, with the lowest in plots with exclosures and bromeliad cover ($0,363 \pm 0,380$ cm). Between the four treatments a significant difference in mean absolute shoot growth was found for species of *A. macrocarpa* using a two-way ANOVA (ANOVA, df = 1, F = 11, 412, P = 0, 005). In Fig. 6 the difference in mean absolute shoot growth in plots were bromeliad is present or absent is large and significant (two-way ANOVA, df = 1, F = 5,364, P = 0,036), as well as the difference between plots with and without an exclosure (two-way ANOVA, df=1, F = 7,045, P = 0,019).

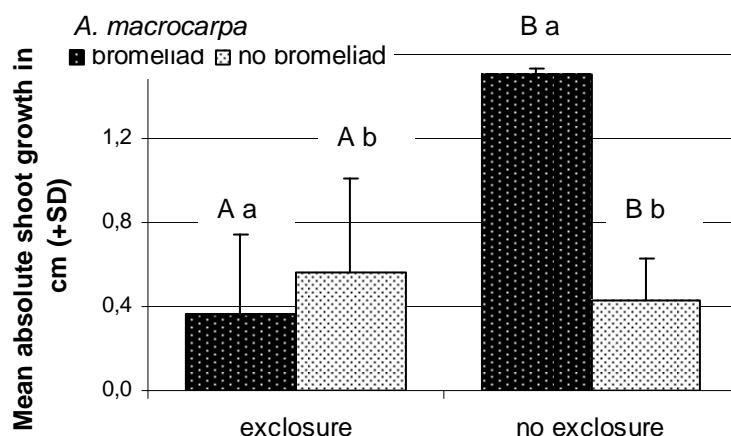


Fig. 6. Mean absolute shoot growth in centimetres of *A. macrocarpa* seedlings between the four treatments (+SD). Capital letters (A or B) indicate the significant difference between plots with and without exclosures and small letters (a or b) show the significant difference between plots with and without bromeliad using a two-way ANOVA. Significance is found when the P-value is < 0,050.

Post Hoc tests were performed to compare the differences in mean herbivory and mean absolute shoot growth between species when data of the four treatments were pooled together (Fig. 7). A Dunett's T3 test was performed as Post-Hoc test for herbivory and a Student-Newman-Keuls test for absolute shoot growth. *M. scleroxylum* and *S. brasiliensis* were excluded in the graph of absolute shoot growth (Fig. 7b).

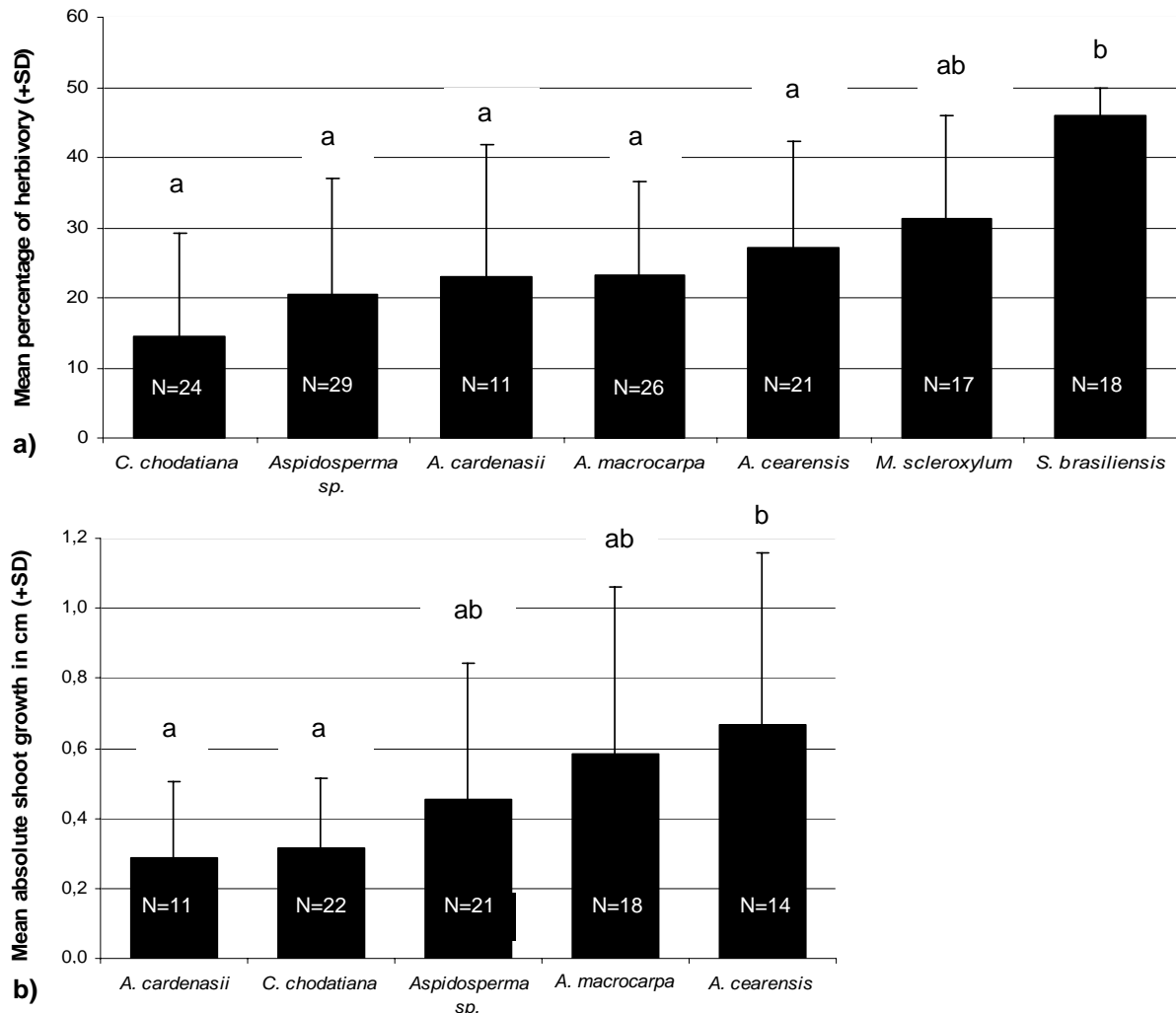


Fig. 7. (a) Mean percentage of herbivory per seedling species (+SD) and (b) mean absolute shoot growth in centimetres per seedling species (+SD). Per species data on herbivory and absolute shoot growth separately were pooled for all plots of all four treatments. Data on absolute shoot growth of *M. scleroxylum* and *S. brasiliensis* were excluded from the analysis. Dunett's T3 Post Hoc test for herbivory and a Student-Newman-Keuls Post Hoc test for absolute shoot growth were used to find significant difference between species. The different letters within each graph (a or b) show these significant differences ($P < 0,050$). In the black columns, N stands for the number of seedlings of which herbivory and growth has been measured. Because the group sizes are unequal, the harmonic mean of the group sizes is used in the analyses ($N = 19,047$ for herbivory and $N = 16,079$ for absolute shoot growth).

C. chodatiana species did experience less herbivory damage in two months ($14 \pm 15\%$), while species of *S. brasiliensis* did experience most herbivory ($46 \pm 4\%$) of all seven species (Fig. 7a). Between *C. chodatiana*, *Aspidosperma sp.*, *A. cardenasii*, *A. macrocarpa* and *A. cearensis* no differences in mean herbivory damage by herbivores were found, while *S. brasiliensis* experienced more damage of herbivores. Species of *M. scleroxylum* did not differ significantly in herbivory damage from all other

species ($31 \pm 15\%$). Mean percentages of herbivory did not show differences between *C. chodatiana*, *Aspidosperma* sp., *A. cardenasii*, *A. macrocarpa* and *A. cearensis*, but mean absolute shoot growth did (Fig. 7b). *A. cardenasii* and *C. chodatiana* grew significantly less in two months ($0,3 \pm 0,2$ cm for both species) than *A. cearensis* ($0,67 \pm 0,49$ cm). *Aspidosperma* sp. and *A. macrocarpa* did not show any difference in mean absolute shoot growth between all five species ($0,45 \pm 0,39$ cm and $0,58 \pm 0,47$ cm respectively).

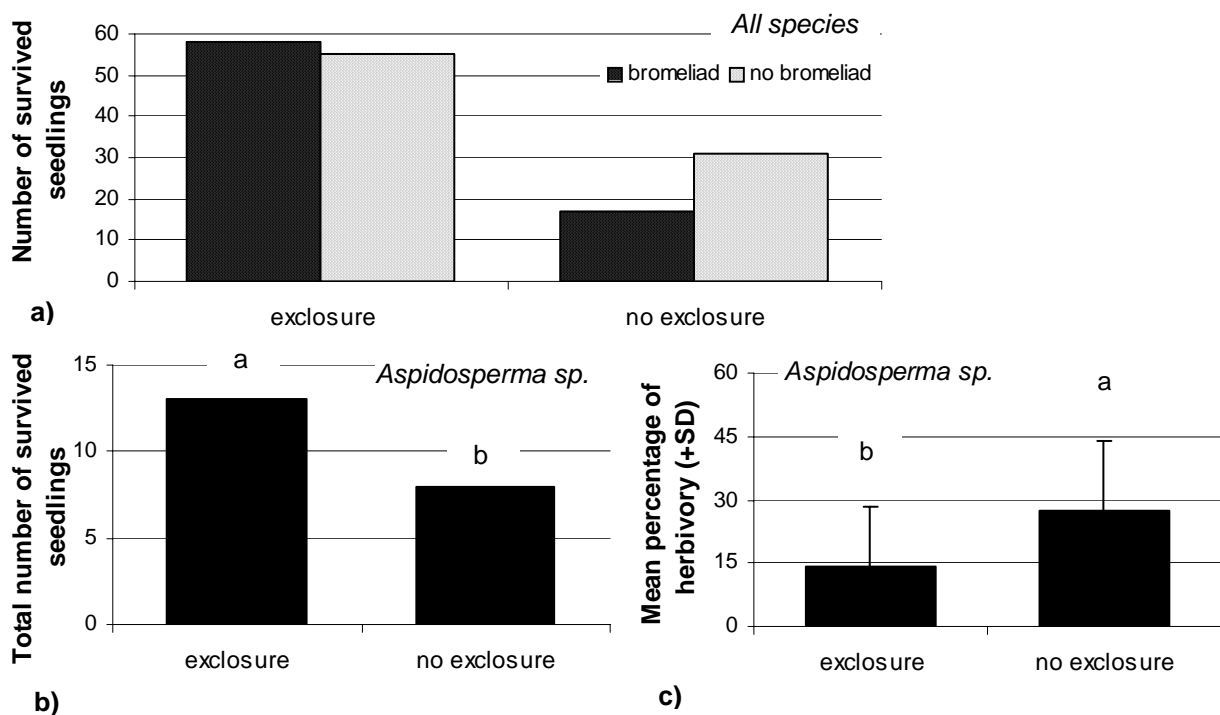


Fig. 8. The influence of bromeliad and exclosures on the survival of seedlings and the influence of only exclosures on survival and herbivory of seedlings. (a) Total number of survived seedlings after two months separated for each treatment, (b) number of survived *Aspidosperma* sp. seedlings pooled separately for plots with and plots without exclosures and (c) mean percentage of herbivory on *Aspidosperma* sp. seedlings pooled separately for plots with and plots without exclosures (+ SD). Columns with different letters (a or b) within a graph are significantly different ($P < 0,050$).

Fig. 8a shows the influence of the four treatments on seedling survival of all seedling species pooled together. In general, more seedlings survived when exclosures were placed around the experimental plots, while in these plots with exclosures the number of survived seedlings did not differ much between the presence and absence of bromeliad (respectively 58 versus 55 seedlings). In plots without exclosures fewer seedlings survived in combination with or without bromeliad. The difference between the presence and absence of bromeliad in these plots without exclosures was larger than for plots with exclosures (respectively 17 versus 31 seedlings). Influences of bromeliad and exclosures on the survival of seedlings could not be tested using Chi-square tests. Chi-square tests could not be computed for the three variables bromeliad, exclosure and survival at once, and therefore the influence of the four different treatments used in the forty experimental plots could not be tested on significance (Fig. 8a). Instead, Chi-square tests were performed for either one of the factors and

survival. Using these crosstabs (survival * bromeliad and survival * exclosure), no significant influences of bromeliad or exclosures on the survival of seedling species were found, except for *Aspidosperma* sp. for which a significant difference was found between plots with and without exclosures (Pearson Chi-square, N = 64, df = 1, Value = 5,688, P = 0,017) (Fig. 8b). For this same species significant differences were found between the mean percentage of herbivory in plots with and without exclosures (ANOVA, df = 1, F = 5,126, P = 0,032) (Fig. 8c). With the presence of exclosures significant more seedlings of *Aspidosperma* sp. survived than when exclosures were absent (13 versus 8 seedlings) and experienced significant less herbivory ($14 \pm 14\%$ versus $27 \pm 17\%$).

Linear regressions were performed to find relations between the environmental variables and herbivory, survival or absolute shoot growth. However, no significant relations of the microhabitat characteristics were found. Significant differences were found analyzing the influence of herbivory on survival and absolute growth using one-way ANOVAs. Herbivory had a significant negative effect on survival (ANOVA, df = 98, F = 24,354, P = 0,000) and on absolute shoot growth (ANOVA, df = 73, F = 2,315, P = 0,031).

Discussion

Seed predation

Seeds of *M. scleroxylum* were discovered much later than those of *C. chodatiana* at each bromeliad density separately. It could be possible that seeds of *M. scleroxylum* were discovered earlier but were not attractive enough to consume. A logic explanation for this could be the fact that seeds of *M. scleroxylum* are wind dispersed (Justiniano & Fredericksen 1998b & 2000b, Pinard *et al.* 1999, Mostacedo & Pinard 2001, Jardim *et al.* 2003, Mostacedo *et al.* 2003) and seeds of *C. chodatiana* are animal dispersed (Fredericksen *et al.* 1999 & 2000, Justiniano & Fredericksen 2000b, Mostacedo & Pinard 2001, Jardim *et al.* 2003, Justiniano *et al.* 2003, Kennard *et al.* 2004). Seed predating animals are not searching for wind dispersing seeds and they prefer animal dispersing seeds. *M. scleroxylum* had a brown seed with a wing (Justiniano & Fredericksen 1998b & 2000b, Pinard *et al.* 1999, Mostacedo & Pinard 2001, Jardim *et al.* 2003, Mostacedo *et al.* 2003) and probably less food reserves, while *C. chodatiana* had bigger and striking orange to dark red seeds (Fredericksen & Justiniano 1998, Fredericksen *et al.* 2000, Mostacedo & Pinard 2001, Jardim *et al.* 2003) which might contain higher energy contents, and according to Janzen (1981) may bright coloured seeds be more visible to some seed predators. *C. chodatiana* seeds could be for these reasons more attractive to seed predators than *M. scleroxylum* seeds. Seed removal agents have been shown to prefer seeds of certain species, which could be related to seed characteristics such as seed size, nutrient contents, local abundance, and handling time (Meiners & Stiles 1997).

Microhabitat characteristics did not show any effects on the discovery time of seeds of the two species. Alcántara *et al.* (2000) have found the same results in their study; no differences in time needed by seed predators to find a depot between microhabitats, but they found a shorter time needed in dense than in sparse vegetated patches. In this study, the bromeliad density did not have an effect on the number of days needed to find a seed depot for each of the two species, but the bromeliad density did have a significant effect between the two species.

According to the hypothesis that bromeliad prevent small seed predators against their own predators, the highest removal rates during the experiment and the highest removal percentages at the end of the experiment were suspected to be found when the ground cover with bromeliad was highest, and the lowest removal rates and percentages were suspected to be found in plots without bromeliad. In this study the lowest removal rates and removal percentages per species were found for plots without bromeliad, but the highest removal rates and removal percentages were found for plots with a low bromeliad density. However, the differences in removal rates between high and low bromeliad densities were not significant, while the differences in removal rates between low and no bromeliad densities were significant. During 30 days the seed removal rate of *C. chodatiana* showed an effect between the presence and absence of bromeliad. Significantly less seeds were predated when bromeliad were completely absent, while there was no significant effect found between a high and low density of bromeliad. The removal rates of *M. scleroxylum* seeds varied significantly between no and low bromeliad densities, but not between high and low or no bromeliad densities. Seed predation rates between the two species differed, and seeds of *C. chodatiana* were not only earlier discovered than *M. scleroxylum* seeds, but were also removed in higher rates during the experiment

and at the end of the experiment the percentage of removed seeds at each bromeliad density was higher as well. After approximately 3 days in plots with bromeliad and after 6 days in plots without bromeliad half of *C. chodatiana* seeds had disappeared and after 30 days almost all seeds were disappeared, while for *M. scleroxylum* seeds it took 30 or more days until half of the seeds was removed. Although the same bromeliad densities were studied between and within the two species, seed predators did have preferences for *C. chodatiana* instead of *M. scleroxylum* seeds, and the presence of bromeliad ground cover plays an important role on the seed removal rate, rather than the density of bromeliad. Brokaw (1983) found that high densities of bromeliad also caused higher seed predation rates, while this is in contrast to studies of Fredericksen & Mostacedo (1998) in which they found that bromeliad cover did not have an effect on seed removal rates. Various studies found that the foraging activity was affected by ground cover in general (Reader & Beisner 1991, Crawley 1992) and that the activities of seed predators were concentrated in structurally complex vegetation (Schupp 1988). Crawley (1992) found that rodents are one of the most important post dispersal seed predators. Rodents preferred habitats with more cover because cover provides a good shelter from predators (Crawley 1992, Wenny 2000, Jones *et al.* 2003), and therefore the concentration of the activity of seed predators in sites with bromeliad could partially explain the high seed removal rates. Another explanation for high seed predation rates at sites with the presence of bromeliad is that these bromeliad provides lower light levels during the day and with this seed predators can have longer activity patterns.

There are large differences in seed characteristics between the two species which can explain the differences in seed removal rates. The most important of all is the difference in dispersal mechanism which brings special characteristics to either of both, such as size, colour and nutrient content. *C. chodatiana* is an animal dispersed seed (Fredericksen *et al.* 1999 & 2000, Justiniano & Fredericksen 2000b, Mostacedo & Pinard 2001, Jardim *et al.* 2003, Justiniano *et al.* 2003, Kennard *et al.* 2004) and the presence of bromeliad is important for seed predators. These animals could have great advantage of the spiny ground bromeliad, because of its protection against predators of their own. As appears from personal observations, armadillos, mice and leaf cutter ants were the most abundant predators of *C. chodatiana* (M. Grol, *personal observations*, 2005) and it could be that these predators are attracted by colour, smell, nutrient content or seed size. It might even be possible that foraging is not depending on the time of the day and foraging activity patterns could be longer, because of protection against their own predators and providence of shade by bromeliad. *M. scleroxylum* seeds are wind dispersed (Justiniano & Fredericksen 1998b & 2000b, Pinard *et al.* 1999, Mostacedo & Pinard 2001, Jardim *et al.* 2003, Mostacedo *et al.* 2003) and do not depend on seed predators that find protection by bromeliad cover, but these seeds depend on wind. Wind-dispersed seeds escape predation by its greater dispersal distance from the parent trees where seed predators may congregate (Janzen 1970). *M. scleroxylum* seeds considered to be removed were most of the time visually infested by insects, such as small ants and beetles (M. Grol, *personal observations*, 2005), and taken away by the observer from the seed depot when they were too much damaged so that germination seemed unlikely. Fredericksen *et al.* (2000) also concluded from their experiments that *M. scleroxylum* seeds were most predated by ants and other insects. Suggesting that most seed

predation was performed by insects and does not occur in high bromeliad densities, insects are not depending on high bromeliad densities for protection. This is in contrast with the results found by Reader & Beisner (1991), they indicated that greater seed predation by ants was found in dense vegetation rather than in less dense. Further seemed it unlikely that seeds were blown away or that seed size might be an important factor to explain seed predation rates, although different assumptions have been made about the influence of seed size on seed removal rates. Some studies stated that predation rates on smaller seeds are greater than on bigger seeds (Alcántara *et al.* 2000, Jones *et al.* 2003), but other studies found that predators removed the largest seeds first (Reader 1993, Gómez 2004, Hulme 1998, Fredericksen *et al.* 2000, Jansen 2003). And unfortunately, the last group found no pattern of predation relative to seed size (Reader 1993). It might also be possible that seed size is related to the type of seed predator, for example small removers such as ants prefer medium to small seeds, while bigger seed predators such as rodents prefer medium to large seeds. Another factor that might affect the predation rate is the abundance of available seeds at the moment, and the distance to the mother tree. The Janzen-model or escape hypothesis (Janzen 1970) predicts that seedlings and young trees growing close to adults should experience higher levels of damage and mortality from herbivorous insects, with the adult trees acting as either an attractant or source of the seed predators and herbivores. Wenny (2000) found also that seed removers and herbivores will forage close to the parent trees where seeds and seedlings are most abundant. If seed predators are density-responsive, they will concentrate their foraging near parent plants where predation rates will be high.

It is difficult to characterize factors affecting seed removal or the distribution of bromeliad through the forest. In this study only a few could explain seed removal rates of *C. chodatiana* and none could explain seed removal rates of *M. scleroxyllum*. Canopy cover had a negative relation with seed removal rates of *C. chodatiana* which means that more seeds were removed when the canopy was more open. This is in contrast with results of Lagos *et al.* (1995) who found that seed predators prefer sites with a dense canopy cover, which provides more shade during the day and may possibly create longer activity patterns. Canopy cover was in this study negatively correlated with the liana density, which suggests that lianas prefer higher light environments. Lianas are characteristic of many tropical forests and grow rapidly in the high-light environments (Appanah & Putz 1984). The canopy cover in this study ranged from 85 to 98 %, with an average of $95 \pm 3\%$. Altitude had a positive relation with the seed removal rate of *C. chodatiana* and with the bromeliad density. More seeds are removed when the altitude increases and with an increasing altitude the density of bromeliad gets higher. Lower bromeliad densities were found at the lower parts in the forest, and high bromeliad densities were found at higher parts in the forest. Fredericksen *et al.* (1999) have found that bromeliad reaches its highest densities on side slopes in medium- or high-light environments, and that they were noticeably absent in forest near rivers and streams with dense overstories. At these drier, upland sites the bromeliad compete effectively for soil moisture through storage of water in leaves and roots (Fredericksen *et al.* 1999). A negative relation was found between altitude and soil moisture content, between altitude and the percentage of herb cover and between altitude and the number of seedlings and the number of seedling species. This suggests that in the lower parts of the forest more water is available in the soil, the forest floor is covered with a higher percentage of herbs, counts more

seedlings and seedling species than in the higher parts of the forest were bromeliad densities and seed removal rates are higher. Herbs and seedlings are depending on water, since water is one of the main factors affecting recruitment patterns in dry forests (Howe 1990). Altitude and bromeliad density both had a positive effect on the mean bromeliad height which suggests that the bromeliad height increases when bromeliad cover increases. And the increasing mean bromeliad height was correlated with a lower density of woody species. This could possibly due to the competition for light. Bromeliad must have been competing for light and grew high in dense bromeliad vegetations, while woody species cannot compete with the growing bromeliad for light and possibly water too.

Dense vegetation was suspected to have an effect on the number of seedlings or the number of occurring seedling species. In North-eastern Mexico, Garcia & Jurado (2003) found a greater number of seedlings under dense thornscrub than under cleared thornscrub. Therefore, these numbers were measured of each plot of the seed predation study and tested. However, from this study it appeared that the bromeliad density had no significant effect on the abundance of seedlings or seedling species. Of the environmental variables only altitude showed a significant correlation. Altitude correlated significantly with the number of seedlings and the number of seedling species. Thus, at higher parts in the forest, where the bromeliad density is higher were less seedlings and seedling species present, while at the lower parts where the ground cover of herbs is higher and more water in the soil is available, more seedlings and seedling species occurred. A possible explanation for this is that bromeliad not only provides shelter for seed predators, but also captures fallen seeds from their mother tree in their rosettes (Brokaw 1983).

In this study, all other factors did not affect the seed removal rate or the distribution of bromeliad through the dry forest INPA. Many other studies have found influences of environmental habitat characteristics on seed removal. Some studies found that seed survival rates were greater in thick than in sparse litter (Fredericksen *et al.* 2000, Peña-Claros & de Boo 2002), while Schupp (1988) found in his study that seed survival was independent of litter quantity. Peña-Claros & de Boo (2002) also found higher survival rates when liana densities or *Cecropia* litter cover were low. And Fredericksen *et al.* (1999) found that light levels influenced the distribution of bromeliad through the forest positively.

Seedling regeneration

By creating four different treatments in the forest, it was suspected to find an influence of bromeliad and exclosures on the herbivory rate, survival and shoot growth of seedlings. Despite these expectations, no significant differences were found for herbivory and shoot growth, and for the influence of a combination of bromeliad and exclosures on survival no statistics could be computed. Instead, separate combinations of bromeliad * survival and of exclosure * survival were tested with Chi-square Crosstabs. Using all three variables at the same time in a Crosstab was not possible in the present study (statisticians, other researchers and students, including myself, were not able to perform, explain and/or help with this in the present study). This means that the influence of the presence or absence of bromeliad and exclosures combined on survival could not be tested on significance, and therefore it is not known if the four treatments had a significant effect on survival.

Either, looking at the graph (Fig. 8a) of these data it could be possible that the presence or absence of exclosures and bromeliad did have an influence on seedling survival. Protecting seedlings from herbivores by placing exclosures did result in more surviving seedlings after two months than in plots without exclosures. In the protected plots, the presence or absence of bromeliad did not seem to have any effect on the number of survived seedlings, which could easily be explained by the fact that herbivores were already excluded from the plots by the exclosures, and it did not matter any more whether or not bromeliad were present for the protection of herbivores. As expected, plots without exclosures had fewer seedlings that survived, and of these plots more seedlings were counted after two months in plots without bromeliad. Now herbivores could enter the plots and bromeliad might have functioned as a protection of these animals, which resulted in less seedlings. Exactly the same results were found by Parker & Salzman (1985) in their study in New Mexico. They found that the removal of plant competitors did not increase survivorship of seedlings when exclosures were placed against herbivores and when exclosures were not present, the removal of competitive vegetation had a positive effect on the survivorship. In the present study it seemed unlikely that the competition for water and/or light between bromeliad and seedlings played a role in seedling survival, because if there was a lot of competition, also a lower number of survived seedlings was suspected in plots with exclosures and bromeliad.

Looking at the influence of only exclosures on herbivory, survival and shoot growth of seedlings, significance was found only for the herbivory damage and survival of *Aspidosperma* sp. seedlings, but not on shoot growth, nor for the other species. More herbivory of *Aspidosperma* sp. took place in plots without exclosures, and significantly more seedlings survived in plots with exclosures. Only for this species, exclosures did have the positive expected effect on survival, and kept herbivores outside the plots which resulted in less herbivory. Exclosures were built to keep mammals outside the plots, but small rodents and insects could still enter the protected areas. During the research many insects were observed within the exclosures, such as ants, beetles, grasshoppers walking branches and caterpillars (M. Grol, *personal observations*, 2004-2005). Because almost no significant effects on herbivory were found between plots with and without exclosures and because many leaf eating insects were observed in plots with exclosures, from this study could be resulted that not only bigger mammals have an impact on the herbivory of seedlings, but insects have great influences too.

The presence or absence of bromeliad did not show significant differences in herbivory, survival and absolute shoot growth among species. The suspected influences of bromeliad on the shoot growth and survival of seedlings as a result of competition for water and light were not found, and also the influences of bromeliad on herbivory and survival as a result of shelter for herbivores was not found. A possible explanation for not finding any effect of the presence or absence of bromeliad in this study is that large areas of the study area contained bromeliad at the beginning of the experiment, and some plots had first to be cleared. Because of the presence of bromeliad at the beginning, a similar herbivory pressure could be expected in the complete study area. For this reason it might be possible that clearing small parts in the large bromeliad area did not have any effect on survival and herbivory of seedlings. Shoot growth might still be influenced by clearing small areas with the upper and lower parts of bromeliad. Clearing these areas means that there is no more competition within the

plots for water and light and shoot growth is still suspected to be higher. Unfortunately, this was not the case; no significant differences were found between plots with and without bromeliad. Although in the present study no effect of bromeliad cover was found on the herbivory, survival and growth of seedlings, other studies did find influences of bromeliad or other types of ground cover. Experimental removing of ground cover significantly increased seedling emergence (Gross & Werner 1982) and Fredericksen & Mostacedo (1998) found that bromeliad did have a negative effect on germination. Brokaw (1983) found that high bromeliad densities did cause higher seedling herbivory levels and suppresses the regeneration of other tree and plant species (Brokaw 1983, Fredericksen *et al.* 1999, Fredericksen & Mostacedo 2000). High densities of bromeliad also create shade as well as other types of ground cover, and shade may inhibit germination, which enables the emerging and growth of other plant species (Brokaw 1983).

Pooling all data of the four treatments together, differences were found between species for the mean percentage of herbivory and mean absolute shoot growth. Differences in herbivory between species were found for *S. brasiliensis*, which suffered significantly more herbivory than the other species, except for *M. scleroxylum* for which no significant difference was found between all species. Herbivory was measured of cotyledons or very young leaves. Young leaves experience the majority of herbivore damage since many herbivorous insects prefer these newly expanded leaves, which are especially vulnerable (Coley 1983), and with this herbivores also might prefer cotyledons. Coley (1983) also found that leaf toughness was correlated with levels of herbivory, and therefore tougher leaves have less predation. This could be two explanations for the high percentage of herbivory found on *S. brasiliensis*. Cotyledons and leaves of *S. brasiliensis* were very small and thin and the seedlings were small as well, while cotyledons and leaves of *C. chodatiana* and *Aspidosperma* sp. were much bigger and tougher and seedlings were larger, and seedlings of *A. cardensisii* had much tougher cotyledons than *S. brasiliensis* (M. Grol, *personal observations*, 2004-2005). Furthermore, leaves of *A. macrocarpa* contain high concentrations of tannin (Justiniano & Fredericksen 1998a), and therefore may not be favoured by herbivores which results in lower herbivory damage. Seedlings of *A. cearensis* grew very fast and after two months the mean absolute shoot growth was highest. This fast growing may provide the seedlings protection against herbivory.

S. brasiliensis and *M. scleroxylum* were excluded from the data set of the mean absolute growth analysis. The five species left did not show any significant difference in mean percentage of herbivory, but did show significant differences in mean absolute shoot growth. *A. cearensis* grew most in two months and *A. cardensisii* and *C. chodatiana* grew fewest in two months. *Aspidosperma* sp. and *A. macrocarpa* did not differ significantly in their absolute shoot growth from the other three species after two months. No measurements were extracted on seed size or seed mass of the species, but according to personal observations of seed sizes (M. Grol, *personal observations*, 2004) a possible explanation for the highest absolute shoot growth of *A. cearensis* could be that this species had the largest seeds. Researchers have found that large seeded species produce the biggest seedlings (Howe & Richter 1982). Although small seeded species produce more seeds for a given amount of effort, seedlings from large seeded species are able to out compete the relatively poorly-provisioned seedlings produced by small seeds, which influences early performance of seedlings (Khurana &

Singh 2001). *A. cearensis* is a light demanding species, as well as *A. macrocarpa* which has the second highest absolute shoot growth, while *A. cardenasii* and *C. chodatiana* together with *Aspidosperma* sp. are shade tolerant species. Shade tolerant species grow more slowly than shade intolerant species, even under high light conditions (Denslow 1987). In general, shade tolerant species germinate, grow and have high survivorship in the forest understorey, while shade intolerant species germinate and grow rapidly in large canopy openings (Poorter 1998). It is possible that seedlings of *A. cearensis* did not only grow more rapidly because it is a shade intolerant species, but also as a result of competition for light. Seedlings within experimental plots might compete between the same and/or different species, since bromeliad cover did show to have no effect at all on seedlings.

None of the microhabitat characteristics in the linear regression models in the present study predicted herbivory pressure, shoot growth or survival of seedlings, while influences were suspected according to the literature. Morris *et al.* (2000) found as a result of increasing shade and irrigation, and with this increasing soil moisture, higher levels of germination. Gerhardt (1998) showed that not only soil environment is important for herbivory, but also light and to a certain extent plant size influences herbivory patterns. Higher light intensities presumably encourage insect activity, and this might increase herbivory. According to Lugo *et al.* (1978) soil moisture is a key factor influencing growth and survival of plant communities in dry forest, and with an increasing light availability growth rates increased (Rincón & Huante 1993, Kennard & Putz 2004) and canopy openness showed a positive relation with seedling survival (Rose 2000). In tropical forests, seedling growth is limited to the rainy season (Rincón & Huante 1993, Gerhardt 1996a, Poorter & Hayashida-Oliver 2000) and the number of herbivores is highest during that season as well (Janzen 1981), which suggests that herbivory is highest when plants grow during the rainy season, and in the dry season seedlings generally experience high mortality, compared with the growing season (Gerhardt 1966b, Lieberman & Li 1992).

Analyzing the influence of herbivory on survival and absolute growth using one-way ANOVAs pooled for all treatments together, a negative effect of herbivory on survival and on absolute shoot growth were found. Thus, more herbivory resulted in a reduced number of survived seedlings and reduced absolute shoot growth as expected. Howlett and Davidson (2003) found these same results; exposure of seedlings to herbivores more than doubled seedling mortality and reduced pioneer growth rates by an average of 44%.

Conclusions

The environment has no effect on discovery time, herbivory, survival and absolute shoot growth, and only altitude and canopy cover had an effect on the removal rate of animal dispersed seeds. The distribution of bromeliad through the forest could only partially be explained by some environmental variables. Altitude seemed to be the most important habitat characteristic and increasing altitude reduced the ground cover with herbs, the number of seedlings, the number of seedling species and soil moisture content, while the bromeliad density and the mean bromeliad height increased. This concludes that the bromeliad is distributed over the higher and drier parts of the forest where less competition is with herbs. In these higher parts of the forest the number of seedlings and seedling species were low as a possible result of the high seed removal rates or as a result of the competition for water and light with the present bromeliad which had a higher mean bromeliad height than in the lower parts of the forest.

Bromeliad densities had no effect on the time of discovering seeds within a seed species, but between a wind dispersed and an animal dispersed seed species differences were found. Animal dispersed seeds were discovered much faster, seeds were removed faster during the experiment and at the end the percentage of removed seeds was higher as well than that of wind dispersed seeds. Seed removers tend to prefer animal dispersed seeds above wind dispersed seeds. Bromeliad cover influenced the removal rates of animal and wind dispersed seeds positively, but the presence of bromeliad seemed to be more important than the density.

Treatments did not affect herbivory and absolute shoot growth, and the effect on survival was not tested on significance. However, removing bromeliad in protected plots showed no effect on seedling survival and removing bromeliad in plots without protection against herbivores resulted in a more survived seedlings. Herbivory appeared to be more important than competition for seedling survival (Parker & Salzman 1985).

Bromeliad or exclosures did not influence herbivory, survival and absolute shoot growth, except for one species, *Aspidosperma* sp., and only this species satisfied to the expectation that placing exclosures should reduce herbivory rates and increase seedling survival. Many insects were signalled inside the exclosures and it is suggested that not only larger mammals are important herbivores, but insects and small rodents which were capable of entering the exclosures also play an important role in herbivory, survival and growth of young seedlings, and therefore no effect of exclosures was found. Furthermore, herbivores did not depend on bromeliad cover for shelter against their predators. Thus, it is not clear if a high bromeliad cover has a negative influence on tree regeneration.

Shade intolerant species experienced higher absolute shoot growth and higher herbivory than shade tolerant species. Light demanding species are fast growing species, which might compete for light against other seedlings, since bromeliad cover did not have any effect. Herbivores prefer young leaves which are not tough (Coley 1983) and this might explain the higher herbivory rate of *S. brasiliensis*. Furthermore, increased herbivory reduced survival and growth of seedlings.

This study supports the hypothesis that seed predation reduces the number of available seeds for germination and with this tree regeneration. However, the presence of bromeliad did not show to have any effect on the herbivory, survival and growth of seedlings and does not effect tree regeneration.

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