

## FOREST MICROSPATIAL HETEROGENEITY AND SEED AND SEEDLING SURVIVAL OF THE PALM *ASTROCARYUM MURUMURU* AND THE LEGUME *DIPTERYX MICRANTHA* IN AN AMAZONIAN FOREST

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**Resumo.** Nós usamos a variação natural ocorrendo nas propriedades de microambientes para examinar como vários fatores afetam a sobrevivência pós-dispersão de sementes e a performance de plântulas já estabelecidas de duas espécies comuns de árvores na Amazônia: a palmeira *Astrocaryum murumuru* e a leguminosa *Dipteryx micrantha*. As observações e experimentos apresentados aqui foram realizados entre Novembro de 1991 e Novembro de 1993 na Estação Biológica de Cocha Cashu, Parque Nacional de Manu, Peru. Em escalas espaciais pequenas, variação no folhicho, vegetação de subosque, e luz incidente teve efeitos significantes somente na sobrevivência de sementes de *Astrocaryum*. A sobrevivência de plântulas de *Dipteryx* foi inversamente relacionada ao número de plantas ao redor delas. O crescimento e sobrevivência de plântulas de ambas as espécies não foi afetado por variações nos componentes bióticos e abióticos dos microambientes, tais como microrelêvo, espessura do folhicho, e a presença de palmeira adulta. Em escalas espaciais maiores a sobrevivência de plântulas de *Astrocaryum* foi inversamente relacionada a densidade de monocotiledoneas de folhas grandes (*Heliconia* spp.) e positivamente relacionada a luz incidente. Mamíferos foram primariamente responsáveis por ambos, a mortalidade de sementes e plântulas. Os resultados deste estudo indicam que a heterogeneidade ambiental criada pelo folhicho, vegetação do subosque, e luz são importantes determinantes de sobrevivência de sementes e plântulas destas duas espécies de árvores com grandes sementes na Amazônia.

**Abstract.** We examined naturally occurring variation in microsites to determine correlates of post-dispersal seed survival and the performance of established seedlings of two common Amazonian tree species: the palm *Astrocaryum murumuru* and the legume *Dipteryx micrantha*. The observations and experiments reported here were made between November 1991 and November 1993 at the Cocha Cashu Biological Station, Manu National Park, Peru. At small spatial scales, variation in leaf litter, understory vegetation, and incident light had significant effects on *Astrocaryum* seed survival. Survival of *Dipteryx* seedlings was inversely related to the number of plants of all species around them. Seedling growth and survival of both plant species were unaffected by variations in the biotic and abiotic components of microsites, such as microrelief, leaf litter thickness, and the presence of an adult palm tree. At larger spatial scales *Astrocaryum* seedling survival was inversely related to the density of broad-leaved *Heliconia* spp. (Heliconiaceae) and positively related to incident light. Mammals were primarily responsible for both seed and seedling mortality. The results of this study indicate that environmental heterogeneity created by leaf litter, understory vegetation and light could be important determinants of offspring survival in these two large-seeded Amazonian tree species. Accepted 10 June 2000.

**Key words:** *Astrocaryum murumuru*, *Dipteryx micrantha*, seed dispersal, seed survival, seedling survivorship, palm, legume, forest heterogeneity, Amazon forest.

### INTRODUCTION

Spatial heterogeneity at various scales affects survival, growth, and differential recruitment of tree seedlings in tropical forests. Gaps represent one very obvious kind of spatial heterogeneity affecting tree recruitment (Ricklefs 1977, Brokaw 1987, Denslow 1987, Brandani *et al.* 1988, Swaine & Whitmore 1988). Gaps contribute significantly to the diversity of tropical forests by allowing the recruitment of light-demand-

ing pioneer species, also the subsequent succession that restores typical mature forest species to the former gap. However, there is growing awareness that a large majority of the adult trees comprising many tropical forests are recruited from advance regeneration where smaller individuals of the vegetation dominants are already present in the forest understory (Fox 1974, 1976; Uhl *et al.* 1988; Whitmore 1989; Clark & Clark 1992). Species comprising advance regeneration germinate under the intact forest canopy and grow slowly until released by the opening of a gap overhead,

typically a gap too small to support heliophilic pioneers. The dominant tall tree species produce seedlings that survive on the forest floor in shade. These will grow rapidly in the presence of gaps that allow sunlight. In the shade, seedlings may persist for many years making little if any growth (Fox 1974, 1976).

Pioneers are scarce because small gaps are far more abundant than large ones in most forests (Cintra & Horna 1997). Experimental studies that have focused on the role of gaps in tree recruitment have typically compared survival and growth of one or more species in gaps as contrasted with the forest understory (Schupp 1988, Cintra & Horna 1997). However, the forest understory is not a uniform environment (Nicoira *et al.* 1999). Biologically significant variation occurs in many parameters, such as available light, microtopography, proximity to conspecific adults, density of understory plants, and depth of leaf litter (Facelli & Pickett 1991, Grubb 1996, Hubbell *et al.* 1999). Given that advanced regeneration contributes a majority of the adult stems in most forests, small scale environmental heterogeneity on the forest floor could contribute to the differential success of species participating in advance regeneration. One variable – thickness of leaf litter – has only recently been investigated. Effects vary with the plant species studied (Schupp 1988; Molofsky & Augspurger 1992; Cintra 1997a,b).

Less well studied is how the presence and amount of litter and vegetation cover might affect the foraging of seed predators that locate their food by olfaction (Price & Jenkins 1986). If thick litter and dense ground vegetation were to hinder detection of seeds by rodents, seed and seedling survival probability could vary with small-scale variation in the amounts of leaf litter and understory vegetation. Results from earlier experiments, conducted in the same area and year, and with the same plant species as the present study (the palm and legume), suggest that leaf litter seed survivorship in the palm *Astrocaryum murumuru* and legume *Dipteryx micrantha* was higher in sites with leaf litter compared with those on bare soil. In natural conditions seed survival was positively correlated with leaf litter (Cintra 1997a). *Astrocaryum* seedling survival was highest in shallow litter, but the *Dipteryx* seedlings were not affected by litter depth (Cintra 1997a). In a 2.5 ha plot, *Astrocaryum* seed predation by insects and mammals is density-dependent. In 1992 a higher proportion of *Astrocaryum* seedlings survived far from, compared with close to, conspecific adult trees, and in 1993 more *Dipteryx*

seedlings survived beneath conspecific adult trees than farther away (Cintra 1997b). In a larger area (100 ha), *Dipteryx* seed survival increased with distance from conspecific adults (Cintra 1997b). In another experiment on a much larger spatial scale (400 ha) it was found that dispersal to tree-fall gaps, and forest objects such as logs and clumps of lianas, would be advantageous for the same plant species (Cintra & Horna 1997, Cintra 1998). However, other components of forest heterogeneity at various spatial scales, such as variation in incident light and density of herbaceous vegetation and their effects on seed and seedling survival, have not yet been investigated, at least in the Amazon forest.

Here we compare survival of the seeds and seedlings of two common, large-seeded tree species, in relation to several parameters of spatial heterogeneity on the forest floor. The mid-story palm, *Astrocaryum murumuru* (Henderson *et al.* 1995), has a mean adult density of 30 individuals per hectare in the floodplain forest at Cocha Cashu (Gentry & Terborgh 1991, Terborgh *et al.* 1993, Cintra 1994). *Dipteryx micrantha* (Brako & Zarucchi 1993), is a canopy emergent, at a much lower absolute density of about 3 per hectare. Both are “keystone plant resources” to the animal community during the annual period of scarcity (Terborgh 1986). Both species have been the subjects of previous research at Cocha Cashu and comparable species have been studied in Panama (Bonacorso *et al.* 1980, Terborgh 1983, De Steven & Putz 1984, Terborgh 1986, Smythe 1989, Forget 1993, Terborgh *et al.* 1993, Terborgh & Wright 1994). *Astrocaryum murumuru* and *Dipteryx micrantha* are similar in the season in which they produce fruits, in size of fruits, seeds and seedlings, and in their secondary seed dispersers and predators (Cintra 1994). In earlier trials we determined that magnetically tagged seeds under fruiting trees were eaten rather than hoarded, such that seed removal is equivalent to seed predation (see Cintra & Horna 1997; Cintra 1997a,b; but see also Forget 1991).

This study is a continuation of others recently published concerning the performance of seeds and seedlings of the same species but at different spatial scales (Cintra & Horna 1997, Cintra 1997a,b; Cintra 1998).

## SITE AND METHODS

The observations and experiments reported here were made between November 1991 and November 1993 at the Cocha Cashu Biological Station, Manu Na-

tion Park, Peru. The total annual rainfall at Cocha Cashu is c. 2000 mm and the mean annual temperature is 24°C. The region experiences a dry season from June to October and a rainy season from November to May. The research was carried out in mature floodplain forest growing on entisols deposited by the whitewater Manur River (Gentry 1990, Terborgh *et al.* 1996).

*Astrocaryum murumuru* is an intensely spiny, monoecious palm that attains heights of up to 20 m (mean 10.0 ± 2.34; n = 40) in the forest mid-story. Flowering occurs during the early wet season (December–January), and fruits ripen at the end of the wet season (March–April). Trees produce 1 to 3 racemes

of about 300 fruits each (Table 1, Cintra 1994). The sweet, apricot-flavored exocarp is eaten by several primates, especially capuchins (*Cebus apella* and *C. albifrons*). Foraging primates knock most of the ripe fruits to the ground beneath the parent tree. Collared and white-lipped peccaries, in addition to squirrels, agoutis, spiny rats, and other rodents, then remove many of the seeds, leaving those that have been invaded by bruchid beetles (Kiltie 1981). Few survive under adult trees, and circumstantial evidence suggests that some palm seedlings arise from scatterhoarded seeds (Kiltie 1981). Germination starts with the appearance of a spiny radicle. The first leaf is produced 1–2 months later.

TABLE 1. Comparison of some characteristics of *Astrocaryum murumuru* and *Dipteryx micrantha* ecology in Cocha Cashu.\*

|                        | <i>Dipteryx</i>                            | <i>Astrocaryum</i>                         |
|------------------------|--|--|
| Phenology              | Annual                                     | Annual                                     |
| <i>Fruits</i>          |  |  |
| Fruiting period        | June–August                                | March–April                                |
| Type                   | Drupe, smooth                              | Drupe, spiny                               |
| Color                  | Green                                      | Orange                                     |
| Fruit crop             | 100 to > 1000                              | 100 to > 500                               |
| Fruit size (cm)        | 3.3 – 6.4 x 2.0 – 4.0 x 1.7 – 3.3 (n = 11) | 4.7 – 6.6 x 2.0 – 2.8 (n = 15)             |
| Pulp width (mm)        | 3.25 ± 0.23 a (n = 6)                      | 3.16 ± 0.87 (n = 15)                       |
| Fruit (Fresh) mass (g) | 27.5 ± 1.40 (15 – 43; n = 24)              | 15.5 ± 2.43 (12 – 19; n = 15)              |
| <i>Seeds</i>           |  |  |
| Size (cm)              | 3.0 – 6.0 x 1.8 – 3.8 x 1.5 – 3.0 (n = 22) | 2.7 – 4.8 x 2.2 – 2.8 x 1.6 – 2.4 (n = 10) |
| (Fresh) mass (g)       | 21.5 ± 2.92 a (8 – 40; n = 11)             | 7.4 ± 1.08 (5.4 – 8.9; n = 11)             |
| <i>Seed dispersal</i>  |  |  |
| Syndrome               | zoochory                                   | zoochory                                   |
| Primary agents         | Bats, monkeys, macaws                      | Squirrel, monkeys                          |
| Distance               | 1 to > 500 m                               | 0.10 to < 30 m                             |
| Secondary agents       | Agoutis, spiny rats, squirrels             | Agoutis, spiny rats, squirrels             |
| Distance               | 1 to > 20 m                                | 1 to > 20 m                                |
| Germination            | September–December                         | September–December                         |
| <i>Seed Predators</i>  |  |  |
| Arboreal               | Macaws, monkeys, squirrel                  | Monkeys, squirrel, insects                 |
| Terrestrial            | Agoutis, spiny rats, squirrels             | Agoutis, rats, squirrel, insects           |
| <i>Seedlings</i>       |  |  |
| Form carpets           | yes, but rarely                            | yes, commonly                              |
| Height (cm)            | 28.96 ± 0.55 (17.5 – 40; n = 54)           | 18.6 ± 0.61 (10 – 25; n = 42)              |
| Stem diameter          | 3.7 ± 2.67 (2.7 – 4.3; n = 31)             |  |
| <i>Adults</i>          |  |  |
| Height (m)             | 46.86 ± 1.48 (24.7 – 62.1; n = 31)         | 10.0 ± 2.34 (7.5 – 18.0; n = 40)           |
| Trunk Diameter (cm)    | 93.19 ± 5.27 (26 – 173; n = 32)            |  |
| Canopy size (m)        | 15 – 20 x 25–30 (n = 30)                   | 4 – 10 x 5 – 10 (n = 12)                   |
| Density (tree/ha)      | 2–6 ind.                                   | 30–35 ind.                                 |

\* Data from Cintra (1994). a = Numbers are mean ± standard error.

*Dipteryx micrantha* is one of the most prominent emergent trees in the forest at Cocha Cashu. Adults had a mean height of  $46.86 \pm 1.48$  m ( $n = 32$ ), though occasional individuals reach 60 m (Cintra 1994). Flowering takes place in November. Fruits, up to 1000 per tree, ripen in May and are removed by bats (especially *Artibeus* spp.) to feeding roosts scattered through the forest (Cintra 1994). Bats chew off the thin, green exocarp and drop the seeds to the ground, where they accumulate in heaps. Rodents then gradually remove the seeds, scatterhoarding some of them. Germination begins in July and continues to October. Germinating seeds remain 1 to 3 weeks with only the radicle emergent, at which stage they are heavily attacked by mammalian seed predators (Table 1, Cintra 1994). Subsequent growth of surviving seedlings to 20–30 cm height is fast and can occur within 1–2 weeks. The cotyledons are dropped within a few days after seedling emergence, leaving two compound leaves with six to ten leaflets each (Cintra 1994).

Both *Astrocaryum* and *Dipteryx* germinate and persist as seedlings under the intact canopy. However, the demographic profile of the two species is markedly distinct. The *Astrocaryum* population structure is relatively symmetric and most individuals are in the intermediate size classes, whereas that of *Dipteryx* is positively skewed, with most individuals in the smallest size classes. Juvenile (pole-sized) individuals are very scarce and rarely recorded even in a significant sampling effort.

*Experiment 1. Survival of naturally occurring seedlings.* We first subdivided the 2.5 ha study plot into 250, 10 x 10 m quadrats in October 1991. The location of the 2.5 ha plot was chosen using random number tables (and picking a number corresponding to a given trail from the many numbered at the Cocha Cashu trail system which comprises c. 400 ha). We tagged and mapped to the nearest 10 cm all individuals of both target species. We did not use all mapped seedlings because of the time needed to check them. Therefore the number of seedlings used was selected with a random number table from those mapped within the 2.5 ha plot. We then revisited the plot five times between October 1991 and September 1992 to record growth and survival of the 116 *Astrocaryum* and 190 *Dipteryx* seedlings used for most analyses. For *Astrocaryum* seedlings, we used the number of new leaves produced over the experimental period. For *Dipteryx* seedlings, we measured increase in height.

A follow-up survey was made in September 1993. Periodic censuses allowed us to distinguish mortality caused by fallen branches and fungus attack from mortality caused by seedling predators. Due to the limited time we had for this study, because we were conducting others experiments at the same time at Cocha Cashu, some of the micro-environmental variables and response variables (growth) were not measured for all seedlings. Because of this the sample size ( $n$ ) in the analyses presented in the results varied depending on the models and variables used.

*Microenvironmental variables*

*Light.* To investigate how microenvironmental variability might affect the survival and growth of seedlings at small spatial scales, we measured the values of several variables within a 20-cm radius around the same 116 *Astrocaryum* and 190 *Dipteryx* seedlings we used to follow survival. We measured the light environment using an Exttech lux meter positioned about 5 cm above each. All measurements were made between 11:00 am and 1:00 pm on overcast days. Meter readings (lux) from the lux-meter were converted to relative values by dividing them by the reading obtained from the unobstructed sky in the middle of a nearby lake. These measurements were made on the same dates as in the forest and about a half hour before finishing the forest measurements.

*Leaf litter.* A 1 m<sup>2</sup> PVC frame (subdivided into 25 x 25 cm squares) was placed 50 cm above each 1 m<sup>2</sup> experimental seed array. The number of 25 x 25 cm subdivisions covered by leaf litter was counted. The proportion covered gave a litter cover index (LCI). We also measured the number of superimposed layers of leaf litter layer at each corner of the PVC frame by forcing a hooked wire through the litter and counting the number of leaves it perforated. Five monthly measurements yielded a mean and variance for the 5-month period, during which leaves fell continuously. These values were used as the leaf litter layer index (LLI).

For some models in the data analysis we scored the number of leaf litter layers as a categorical variable (low = 0 to 2, medium = 3 to 5, high = 6 to 9 leaf layers).

*Presence, density, and cover of understory vegetation.* For experiment 2 (on seed survival, see below), we used a 1 m<sup>2</sup> PVC frame subdivided into 25 x 25 cm squares to estimate ground layer cover from a height of 0.5 m. We counted the number of squares occupied

by *Heliconia* spp., *Tectaria insignis*, an abundant fern, and all other plants. For experiment 1 (on seedling survival), we recorded whether each *Astrocaryum* and *Dipteryx* seedling was under a *Heliconia* sp., *Tectaria*, or neither, as well as the number of ground-layer plants of all other species within a 20-cm radius of each seedling. Because of the lack of time we recorded other species around each seedling for 115 *Dipteryx* seedlings (and about the same number of *Astrocaryum* seedlings used).

*Experimental seeds.* During two weeks in May 1992 we collected seeds of both species along trails, from bat roosts, and beneath fruiting trees at least 1 km from experimental plots. Collected seeds were washed free of debris and dried in the sun. Each seed was tested by floating, weighing, shaking and examining it for holes and scratches produced by seed predators. Only seemingly viable and undamaged seeds were used in the experiments.

Experimental seeds were indelibly marked with a small letter "E" to differentiate them from naturally occurring seeds already present on the forest floor. The seeds were checked for survival weekly for 14 to 20 weeks (for *Dipteryx* and *Astrocaryum* respectively), or until all the seeds at a site had been opened or removed by mammals. Once a week we searched within a 3–10 m radius for seeds that had been displaced from the initial position. When there were naturally occurring seeds of either species at experimental sites we removed as many as necessary to prevent an artificial increase in the local seed density as a result of adding experimental seeds. Fruiting activity in the forest at large was low during the period of the experiment, so that keystone species, including *Astrocaryum* and *Dipteryx*, were especially attractive to vertebrate consumers (Terborgh 1986).

#### Experimental design

*Astrocaryum seed survival.* To test the effect of local seed density on seed survivorship we set out 20 replicates of 4, 8, 16, and 32 *Astrocaryum* seeds per 1 m<sup>2</sup>, at sites arrayed within the 2.5-ha plot within which all *Astrocaryum* and *Dipteryx* plants of all sizes had been mapped and tagged. These 1-m<sup>2</sup> seed presentation sites were placed in the four corners of 10 x 10 m quadrats, which, in turn, were located at regular 20-m intervals along four parallel 100 m transects 20 m apart.

*Dipteryx seed survival.* The corresponding experiment with *Dipteryx* employed the same design except that

10 replicates of each seed density were used with seeds set out in only ten 10 x 10 m quadrats (vs. 20 for *Astrocaryum*) because the seed supply was limited. The quadrats were also located at 20-m intervals along two parallel 100-m transects 20 m apart and intercalating the transects with *Astrocaryum* seeds. All *Astrocaryum* and *Dipteryx* experimental seeds were placed in the quadrats on 20 June 1992. Observations commenced on 27 June. For both *Astrocaryum* and *Dipteryx* we compared whole survival curves and associated covariates measured at the corners and centers of the 1-m<sup>2</sup> plots containing the seed sets. We also examined the time to 50% mortality (weeks) because seed predators may be differentially attracted to small vs. large concentrations of seeds.

*Statistical analysis.* Multiple regression analysis (SYSTAT, Wilkinson 1991) was used to investigate whether biotic and abiotic features of the microsites around the seedlings affected seedling growth. We also used logistic regression analysis (SAS 1987) to investigate how microsite variables affected seedling survival in both species. In these models, the response variable was binary, i. e., whether seedlings survived or had died one year after tagging.

Two-way ANOVA was used to investigate whether the response variable "time to 50% survival (weeks)," was affected by variation in seed density, both within and between plant species. Pearson correlation analysis was used to investigate the degree of correlation among microsite variables. We found that total vegetation cover was highly correlated with *Heliconia* cover. Total vegetation cover was therefore not used in the analysis. We used multiple regression analysis to assess whether time to 50% seed survivorship for the two plant species was affected by leaf litter, ground-layer cover, and seed density.

To investigate the effects of microenvironment (covariates), we fitted a Cox proportional hazard model available in SPLUS (1991) to seed survival curves. This analysis combines all censuses into a single test, correctly encompassing right-censored data, i. e., seeds alive at the end of the experiment for which survival times are unknown. In a complementary analysis, we used both the Mantel-Haenzel test (Log-Rank test), and Peto-Peto's test (a modification of the Gehan-Wilcoxon test) to compare survival functions across seed density treatments, since the former test weights longer survival while the latter emphasizes early survival (SPLUS 1991).

## RESULTS

*Seedling growth and survival of Astrocaryum and Dipteryx.* There were weak and non-significant correlations among the six variables measured at the *Astrocaryum* seedling microsites. None of the factors significantly affected *Astrocaryum* seedling growth (Multiple regression analysis,  $r^2 = 0.063$ ;  $n = 61$ ;  $F = 0.743$ ;  $P = 0.594$ ), or survival of seedlings after one year (Logistic regression analysis, Partial regression for leaf litter, Wald test:  $\chi^2 = 2.55$ ,  $P > 0.05$ , for presence of the other plants:  $\chi^2 = 1.98$ ,  $P > 0.05$ , and for presence of adult palms:  $\chi^2 = 2.60$ ,  $P > 0.05$ ).

Two variables, the presence of *Heliconia* spp. and seedling growth, were used in separate models for *Astrocaryum* seedling survival. This was due to a small number of cases of both variables relative to the other microenvironmental variables used. Neither seedling growth nor shading by *Heliconia* herbs affected *Astrocaryum* seedling survival (Logistic regression for growth, Wald test:  $\chi^2 = 1.22$ ,  $n = 61$ ,  $P = 0.269$ , for *Heliconia* shading effects:  $\chi^2 = 0.129$ ,  $n = 116$ ,  $P = 0.719$ ).

*Dipteryx seedlings.* There were non-significant correlations among the microenvironmental variables used in the models for analysing survival of *Dipteryx* seedlings. *Dipteryx* seedling growth was not correlated with any of the variables ( $R^2 = 0.068$ ;  $n = 82$ ;  $F = 0.453$ ;  $P = 0.479$ ). Of all the factors, only the number of woody plants within a 20-cm radius around *Dipteryx* seedlings had significant effects on *Dipteryx* seedling survival (Logistic regression analysis for abundance of plants, Wald test [ $\chi^2 = 4.83$ ,  $n = 115$ ,  $P < 0.05$ ]). The effects of two variables, incident light and *Heliconia* cover on *Dipteryx* seedling growth, were investigated with a different model and together with *Dipteryx* seedling growth to investigate their effects on *Dipteryx* seedling survival. Shading produced by the large-leaved *Heliconia* herbs did not affect *Dipteryx* seedling survival (Logistic regression for *Heliconia* herbs, Wald test [ $\chi^2 = 0.353$ ,  $n = 115$ ,  $P = 0.552$ ]). Both incident light and *Dipteryx* seedling growth had significant positive effects on *Dipteryx* seedling survival (Logistic regression for incident light:  $\chi^2 = 3.818$ ,  $n = 105$ ,  $P = 0.051$ , for growth:  $\chi^2 = 6.098$ ,  $n = 105$ ,  $P = 0.013$ ). However, faster growing *Dipteryx* seedlings in better illuminated microsites were more vulnerable to browsing by vertebrate herbivores. Due to the small sample size *Dipteryx* seedling growth was not used as a dependent variable. Therefore we were not able to verify the effects of other variables on *Dipteryx* seedling growth.

*Seedling survival at a larger spatial scale.* At a larger spatial scale, that is, when the microsite parameters were measured not close to each seedling but at the corners of the 10 x 10 m quadrats (considering the entire area of the 2.5 ha plot), none of the independent variables had significant effects on *Astrocaryum* seedling growth (Multiple regression analysis:  $R^2 = 0.17$ ,  $n = 19$ ,  $F = 0.53$ ,  $P = 0.745$ ). However, three of these variables (mean *Heliconia* density, mean incident light, and *Astrocaryum* seedling density) had significant effects on *Astrocaryum* seedling mortality (Multiple regression analysis:  $R^2 = 0.55$ ;  $n = 23$ ;  $P = 0.013$ ; Fig. 1) suggesting that a higher number of *Astrocaryum* seedlings survived in more illuminated sites (Partial regression: 1.18,  $P < 0.001$ ), and in sites with higher densities of *Astrocaryum* seedlings (Partial regression:  $-0.024$ ,  $P < 0.05$ ) and high densities of *Heliconia* herbs (Partial regression:  $-0.121$ ,  $P < 0.05$ ). Due to the small sample size at a large spatial scale (few 10 x 10 m with *Dipteryx* seedlings) we did not present results for *Dipteryx* seedlings. After one year, *Astrocaryum* seedlings experienced less mortality (7%) than *Dipteryx* seedlings (39%). Most seedling mortality was attributable to mammalian herbivores, as indicated by stems cut at base or complete removal of the seedling. Few seedlings (< 1%) of either species died from fungus attack. A few seedlings were found covered by dead fallen branches, but still alive. We found no evidence of seedlings being killed by fallen branches.

*Astrocaryum and Dipteryx seed survival.* Only 9% (108 out of 1200) of *Astrocaryum* seeds survived 20 weeks, neither being removed by rodents nor attacked by insects. Even fewer *Dipteryx* seeds (5% or 32 out of 600) survived 14 weeks (Fig. 2).

*Astrocaryum* seed survival was significantly higher in microsites with better illumination, greater leaf litter cover, and greater vegetation cover (Table 2). Survival of *Dipteryx* seeds was not affected by variation in any of the measured microsite parameters. There were no significant differences in the number of weeks to 50% survival at the four seed densities (Two-way ANOVA:  $F = 1.346$ ,  $P > 0.05$ ). *Astrocaryum* seeds survived significantly longer periods ( $F = 10.523$ ,  $DF = 1$ ,  $P < 0.001$ , Fig. 2). Significant differences between *Astrocaryum* and *Dipteryx* were obtained at all seed densities when early survival (Wilcoxon's test:  $\chi^2 = 20.3$ ,  $DF = 3$ ,  $P < 0.0001$ ) or later survival was examined (Log-rank test:  $\chi^2 = 22.6$ ,  $DF = 3$ ,  $P < 0.00004$ ).

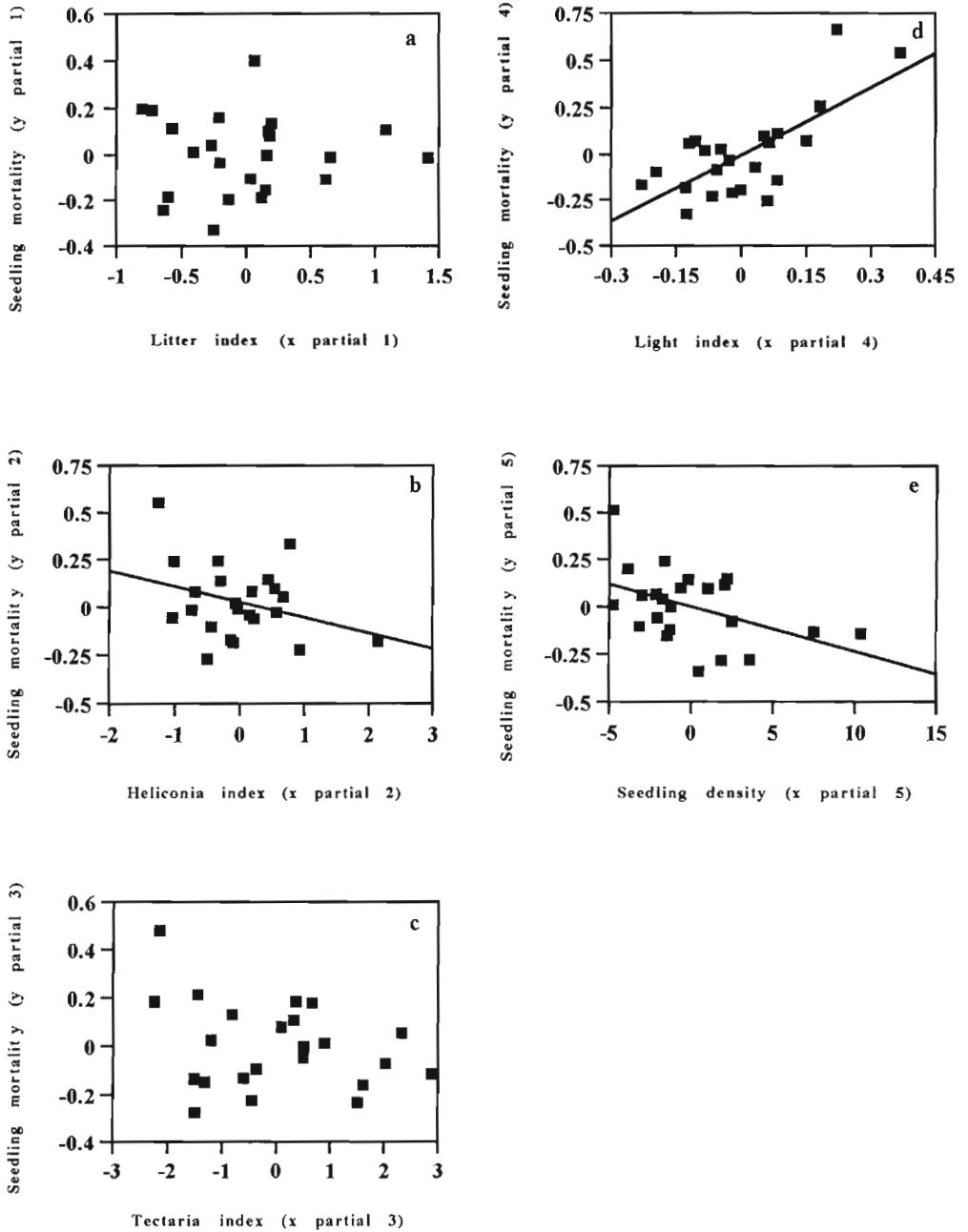


FIG. 1. *Astrocaryum* seedling mortality as a function of (a) mean litter layer, (b) mean *Heliconia* density (plants/m<sup>2</sup>), (c) Mean *Tectaria* density (plants/m<sup>2</sup>), (d) mean light incidence, and (e) *Astrocaryum* seedling density (seedlings / 10 x 10 m). Figures indicate partial regressions. Negative values indicate negative residuals from the models including all other variables.

Spatial variation in leaf litter cover and thickness, and in the cover of *Heliconia* spp. and *Tectaria*, had no significant effects on time to 50% survival of *Astrocaryum* (Multiple regression analysis:  $R^2 = 0.09$ ,  $n = 80$ ,  $P > 0.05$ ) and *Dipteryx* seeds ( $R^2 = 0.13$ ,  $n = 40$ ,  $P = 0.564$ ). *Astrocaryum* seeds survived significantly longer at microsites with higher densities of seeds (Partial regression  $T = 2.4$ ,  $P < 0.05$ ).

## DISCUSSION

The seeds of tropical trees are dispersed into a patchy environment in which a small number of microsites are likely to be optimal for survival, growth and eventual establishment. Small seeds (1 mm or less), such as those from most pioneer tree species, tend to remain dormant until conditions for germination arise (Garwood 1989). Small seeds are also rapidly incorporated into the soil seed bank, which presumably makes them less vulnerable to seed predators. Large seeds, such as those of *Astrocaryum* and *Dipteryx*, that are more easily detected, are exposed to strong predation pressure by mammalian seed-eaters (Janzen 1970; Smythe 1989; Forget 1993, 1996; Terborgh *et al.* 1993; Cintra 1997a,b).

Few studies in the tropics have investigated how a given microenvironmental factor, alone or in conjunction with other factors, affects seed or seedling

survival (see Schupp 1988, Denslow *et al.* 1991, Molofsky & Augspurger 1992, Cintra 1997a). The scale at which factors affect seed and seedling survival will depend on the plant species and properties of the macro- and microenvironment where propagules establish. For example, variation in the size and internal structure of tree-fall gaps, distribution of understory vegetation, and spatial variation in the amount of leaf litter, have been demonstrated to affect seed and seedling survival (Denslow 1980, Brokaw 1987, Schupp 1988, Denslow *et al.* 1991, Cintra & Horna 1997, Cintra 1997a).

The results of this study indicate that leaf litter, vegetation cover, and the amount of incident light affected seed survival of *Astrocaryum* at small spatial scales, that is a few centimeters around the seed. Seeds of *Astrocaryum* and *Dipteryx* had different chances of survival in similar microsites. Some microsites were safer than others for *Astrocaryum* seeds, but not for *Dipteryx* seeds. If most surviving seeds germinate, a higher number of *Astrocaryum* seedlings would be expected to occur in the area. In fact, the number of *Astrocaryum* seedlings in the area is at least five times that of *Dipteryx* seedlings.

Mammal predation on seeds and seedlings of *Astrocaryum* and *Dipteryx* is the main factor in the survival of propagules of both species. Fewer than 10% of the seeds set out at the beginning of the

TABLE 2. Survival of *Astrocaryum* and *Dipteryx* seeds in relation to six environmental component variables (covariate) of the microsites where seeds were placed (Cox Proportional Hazard Regression).

| Parameter Level      | DF | Regression Coefficient (SE) | z      | P   |
|----------------------|----|-----------------------------|--------|-----|
| <i>Astrocaryum</i> + |    |                             |        |     |
| <i>Heliconia</i>     | 6  | -0.019 (0.186)              | -0.102 | ns  |
| <i>Tectaria</i>      | 6  | 0.286 (0.234)               | 1.218  | *   |
| Litter cover (LCI)   | 6  | 1.963 (0.432)               | 4.540  | *** |
| Litter layer (LLI)   | 6  | -0.247 (0.046)              | -5.367 | *** |
| Light                | 6  | 1.147 (0.231)               | 4.966  | *** |
| Seed density         | 6  | -0.016 (0.003)              | -5.370 | *** |
| <i>Dipteryx</i> ++   |    |                             |        |     |
| <i>Heliconia</i>     | 6  | -0.434 (0.865)              | -0.502 | ns  |
| <i>Tectaria</i>      | 6  | -0.807 (0.624)              | -1.293 | ns  |
| Litter cover (LCI)   | 6  | -0.222 (0.188)              | -1.180 | ns  |
| Litter layer (LLI)   | 6  | 0.017 (0.644)               | 0.261  | ns  |
| Light                | 6  | 0.588 (0.328)               | 1.796  | ns  |
| Seed density         | 6  | -0.004 (0.005)              | 0.887  | ns  |

\*\*\*:  $P < 0.0001$ ; \*\*:  $P < 0.001$ ; \*:  $P < 0.05$ ; ns: not significant; +: Likelihood ratio test = 97.4, DF = 6,  $P < 0.0001$ ; ++: Likelihood ratio test = 11.5; DF = 6,  $P < 0.0739$ ; (SE) = standard error.



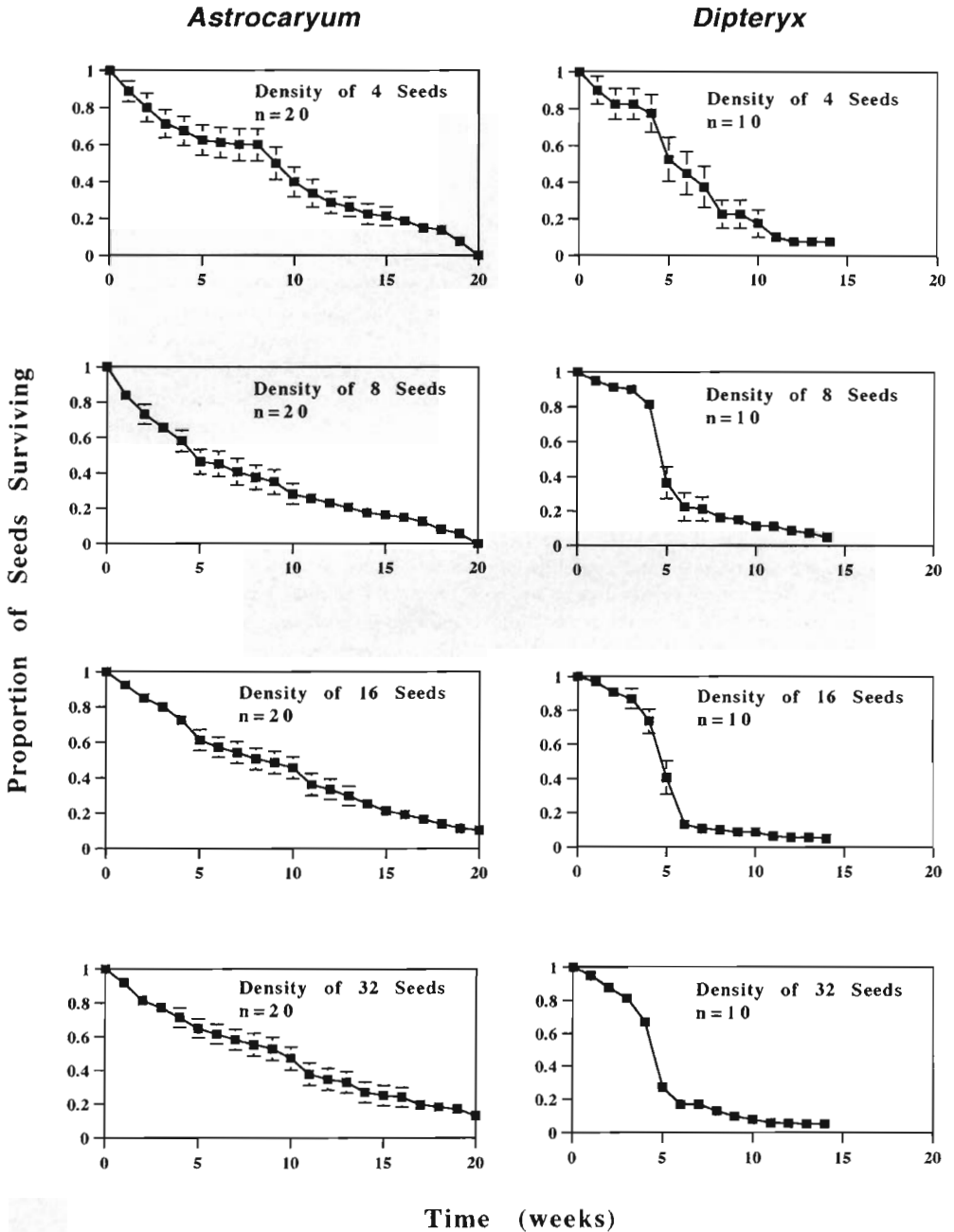


FIG. 2. Survival of *Astrocarylum* and *Dipteryx* seeds over 20 weeks, June to November, of 1992. Values shown represent means with one standard error (vertical bars) of the proportion of seeds surviving in the replicates (twenty for *Astrocarylum* and ten for *Dipteryx*) of each one of four experimental seed numbers (4, 8, 16, and 32 seeds).

experiment remained after 20 weeks. *Dipteryx* seedlings seem particularly vulnerable to herbivory during germination, whereas *Astrocaryum* seedlings, being tougher and spiny, experience less post-germination herbivory.

*Astrocaryum* seedlings could be characterized as shade tolerant (sensu Swaine & Whitmore 1988), because they survive in the poor light environment of the understory until a tree-fall gap is formed nearby (Cintra 1994). Neither species' seedlings were strongly affected by vegetation cover, or leaf litter, although *Dipteryx* seedlings grew faster in better illuminated microsites (see also Clark & Clark 1985, De Steven 1988). However, faster growing *Dipteryx* seedlings were especially subject to herbivore attack (Cintra & Terborgh, pers. obs.), so the early juvenile stage seems to be a bottleneck for this species. Such a conclusion is supported by the paucity of pole-sized *Dipteryx* in the population.

The survival of *Astrocaryum* seedlings appears to depend on larger spatial scales (10 x 10 m quadrats) than those of the microsites around a given *Astrocaryum* seedling. This indicates that offspring survival might be related to the spatial scales at which the seed and seedling predators operate, a result also found for *Dipteryx panamensis* in Costa Rica (Clark & Clark 1984, 1987).

In this study, seed and seedling survival probabilities were found to be a function of several factors acting at larger spatial scales, such as: seedling density, variation of incident light, and the density of the vegetation cover produced by other plant species. A high density of understory herbs can increase shading and competition for light and nutrients, but may also reduce detection by seed predators (Denslow *et al.* 1991, De Steven 1991). In a Costa Rican rain forest, limited light is suggested as a significant factor affecting the growth and survival of plants growing at light levels close to their photosynthetic compensation point (Denslow *et al.* 1991).

The fact that fewer *Astrocaryum* seedlings survive in better illuminated sites reflects a possible preference of herbivores for well-illuminated foraging sites (Price & Jenkins 1986). At Cocha Cashu, we observe that deer forage in small, well illuminated gaps, perhaps because of the higher probability of finding recently established seedlings than in the dark understory (Cintra & Terborgh, pers. obs.). *Astrocaryum* seedling survival is greater at higher *Astrocaryum* seedling densities, which suggests that the best conditions for *Astrocaryum* seedlings are marked by the presence of seedlings that established in previous years.

In general, the results suggest that the establishment patterns of both tree species depend on biotic and abiotic factors, the most important of which are the high post-dispersal seed predation and the properties of microsites. The relative importance of these effects differs for the two plant species.

Finally, establishment of *Astrocaryum* and *Dipteryx* is affected in different ways by environmental heterogeneity created by leaf litter, vegetation cover and light at different spatial scales. Resistance to external circumstances may be conferred by seed reserves. However, in subsequent years, seedling performance must result from the ability of seedlings to grow and survive in the microhabitat. More *Astrocaryum* seeds pass intact through the critical period (the dry season or when most of the vertebrates rely on them for food supply). *Astrocaryum* might survive better and be more abundant than *Dipteryx* simply because of the much greater number of seedlings produced every year. Forest objects are other factors that have been demonstrated to affect seedling performance. Seedlings of at least three palm species (*Iriartea deltoidea*, *Astrocaryum murumuru* and *Attalea cephalotes*) have higher survivorship if their seeds are dispersed by animals closer to logs (Kiltie 1981, Cintra 1998).

Transplanting seedlings to different microhabitats (Losos 1995) would allow an assessment of seedling ability to change the microenvironment and an examination of the effects on future seedling performance and frequency of recruitment.

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## REFERENCES

- Bonacorso, F.J., Glanz, W.E., & C.M. Sanford. 1980. Feeding assemblages of mammals at fruiting *Dipteryx panamensis* (Papilionaceae) trees in Panama: seed predation, dispersal, and parasitism. *Rev. Biol. Tropical* 28: 61–72.
- Brako, L., & J.A. Zarucchi. 1993. Catalogue of the flowering plants and gymnosperms of Peru. Missouri Botanical Garden.
- Brandani, A., Hartshorn, G., & G. Orians. 1988. Internal heterogeneity of gaps and species richness in Costa Rica tropical rain forest. *J. Trop. Ecol.* 4: 99–119.
- Brokaw, N. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology* 75: 9–19.
- Clark, D.B., & D.A. Clark. 1984. Spacing dynamics of a tropical tree: evaluation of the Janzen-Connell model. *Amer. Nat.* 124: 769–788.
- Cintra, R. 1994. Factors affecting post-dispersal seed and seedling survival of two tree species in the Amazon forest. PhD dissertation, Duke University, Durham, NC, USA.
- Cintra, R. 1997a. Leaf litter effects on seed and seedling predation of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in Amazonian forest. *J. Trop. Ecology* 13: 709–725.
- Cintra, R. 1997b. A test of the Janzen-Connell model with two common tree species in Amazonian forest. *J. Trop. Ecology* 13: 641–658.
- Cintra, R. 1998. Sobrevivência pós-dispersão de sementes e plântulas de três espécies de palmeiras em relação a presença de componentes da complexidade estrutural da floresta amazônica. Pp. 83–98 in C. Gascon & P. Moutinho (eds.). *Floresta Amazônica: Dinâmica, Regeneração e Manejo*. INPA, Manaus, Brasil.
- Cintra, R., & V. Horna. 1997. Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in gaps in Amazonian forest. *J. Trop. Ecology* 13: 257–277.
- Clark, D.B., & D.A. Clark. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66: 1884–1892.
- Clark, D.B., & D.A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a Neotropical rainforest emergent tree. *Biotropica* 19: 236–244.
- Clark, A.D., & D.B. Clark. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecological Monographs* 62: 315–344.
- De Steven, D. 1988. Light gaps and long-term seedling performance of a Neotropical canopy tree (*Dipteryx panamensis*, Leguminosae). *J. Trop. Ecology* 4: 407–411.
- De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72: 1076–1088.
- De Steven, D., & F.E. Putz. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43: 207–216.
- Denslow, J. 1980. Gap partitioning among tropical rain forest trees. *Biotropica* 12: 47–55.
- Denslow, J. 1987. Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* 18: 431–451.
- Denslow, J.S., Newell, E., & A.M. Ellison. 1991. The effects of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23: 225–234.
- Facelli, J.M., & S.T.A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57: 1–32.
- Forget, P.M. 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparisons with *Myoprocta exilis*. *Tropical Ecology* 32: 155–167.
- Forget, P.M. 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94: 255–261.
- Forget, P.M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *J. Trop. Ecology* 12: 751–761.
- Fox, J.E.D. 1974. Dipterocarp seedling behaviour in Sabah. *Malayan Forester* 36: 205–214.
- Fox, J.E.D. 1976. Constraints on the natural regeneration of tropical moist forest. *Forest Ecology and Management* 1: 37–65.
- Garwood, N. 1989. Tropical soil seed banks: A review. Pp. 149–209 in Leck, M.A., Parker, V.T., & R.L. Simpson (eds.). *Ecology of soil seed banks*. New York.
- Gentry, A.H. 1990. Four Neotropical rainforests. London.
- Gentry, A.H., & J. Terborgh. 1991. Composition and dynamics of the Cocha Cashu "Mature" floodplain forest. Pp. 542–564 in A.H. Gentry, (ed.). *Four Neotropical rainforests*. London.
- Grubb, P.J. 1996. Rainforest dynamics: the need for new paradigms. Pp. 215–233 in Edwards, D.S., Choy, S.C., & F. Booth (eds.). *Tropical rainforest research: current issues*. Dordrecht.
- Henderson, A., Galeano, G., & R. Bernal. 1995. Field guide to the palms of the Americas. Princeton.
- Hubbell, S., P. Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., & S.L. de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283: 554–557.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *Amer. Nat.* 104: 501–528.
- Kiltie, R. 1981. Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* 13: 141–145.
- Losos, E. 1995. Habitat specificity of two palm species: experimental transplantation in Amazonian successional forests. *Ecology* 76: 2595–2606.
- Molofsky, J., & C.K. Augspurger. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73: 68–77.

