FACTORS AFFECTING POST-DISPERSAL SEED AND SEEDLING SURVIVAL OF COMMON TREE SPECIES IN THE AMAZON FOREST

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Dissertation submitted in partia! fulfillment of the requirements for the.dêgree of Doctor ofPhilosophy in,the Department of ZoQ],pgfjn,the Graduate School - ọ̃ Dü! õ University

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ABSTRACT

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ABSTRACT

Most plants colonize new or disturbed habitats through succesful seed dispersai and seedling establishment. A thorough grasp of these central processes, especially their spatial components, is crucial to understand the distribution and abundance of a plant species. In a three-year study of two common Peruvian rain forest trees, the palm ***Astrocaryum murumuru*** (Mart) and the legume ***Dipteryx micrantha,*** I investigated how physical and biological factors act at different spatial scales to affect post-dispersal seed and seedling survival. I simulated seed and seedling dispersai using experimental seeds and seedlings in the field. Seed and seedling performance and survival were followed from 1991 until 1993 and analyzed using standard statistical methods of survival analysis.

In the first chapter, I investigate whether 'safe sites' exist for ***A. murumuru*** or ***D. micrantha*** seeds or seedlin_gs and what factors determine these sites. At a small spatial scale (1 m^2 plots), leaf litter quantity and light penetration affected seed survival. Toe forest floor provided numerous safe sites for ***Astrocaryum*** and few for ***Dipteryx. Dipteryx*** survival was lôwest insites with the highest surrounding plant density (all plants), suggesting sensitivy to light or nutrient competition.

One important source of environmental heterogeneity in a tropical forest is leaf fall; its depth and quality may vary widely over short distances. Chapter two describes the effects of natural and experimentally mod.ified leaf litter depth on seeds and seedlings. Seed survival of both species was found to be enhanced by the presence and thickness ofleaf litter.

Chapter three focuses on how seedling survival is affected by distance to the parent tree and the local density of conspecific seedlings. This experiment provides a test of the still controversial Janzen-Connel m del (Janzen 1970, Connel 1971) for these two species. In general my results support the model. ***Astrocaryum*** seed and seedling survival were respectively density and distance-dependent in relation to adult trees. ***Dipteryx*** seed and seedling survival showed distance-dependence only.

Finally, chapter four examines the importance of tree-fall gaps to the success of ***Astrocaryum*** and ***Dipteryx*** seeds and seedlings. I compared the performance of seeds and seedlings placed in gaps and in closed forest to test the colonization hypothesis of Howe and Smallwood(1982).

Both species showed increased seed survival in tree-fall gaps. In conclusion, seed dispersai is advantageous for these two tree populations. Patterns of seed and seedling survival were complex and dependent on multiple factors such as offspring age (seed or seedling), spatial scale, qualities of microsites, type of habitat, distance from a conspecific adult, presence of gap, type of predator and year considered.

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INTRODUCTION

1- A REVIEW Of SEED DISPERSAL THEORY

The study of dispersa! is central to plant ecology because it is uniquely through this process that plants can colonize new sites. Some of the most important factors influencing the evolution of dispersa! are spatial and temporal variation in habitat quality (Gadgil 1971, Roughgarden 1979). Theoreti.cal models have suggested that dispersa! is advantageous (Roughgarden 1979, Hoivitz and Schemsky 1986, Murray 1986) even in stable habitats and under conditions of high mortality (Hamilton and May 1977). Seed dispersai to a favorable site and the subsequent seedling establishment at that site are crucial steps in trees' life cycles (Harper 1977).

Classical studies of seed dispersai and seed and fruit biology conducted between the 1930's and 1960's were concemed with questions related to biogeography and migration processes of plant species (Ridgley 1930, van der Pijl 1969). Later studies, based on fruit and seed morphology, attempted to infer the effectiveness of plant dispersai by assuming that the presence of any conspicuous dispersa! mechanisms is ultimately a result of continuing selection to establish offspring at some distance from the parent plant (Stebbins 1974). Both biogeographical and evolutionary approaches primarily focused on long-distance dispersai and colonization of remote sites with little attention to actual recruitment.

Quantitative population studies at local leveis have also suggested that most plants have evolved seed dispersai mechanisms that enable offspring to establish at some distance from the parents (Janzen 1970, van der Pijl 1972, Harper 1977, Cook 1980, Fenner 1985, Murray 1986, Janson 1992).

The propagation of seeds through the environment may have important demographic consequences for species distribution and abundance, since seed dispersai affects patterns in seedling establishment, and consequently adult distribution (Janzen 1970, Connell 1971, Howe and Smallwood 1982, Clark and Clark 1984, Howe 1991). Therefore the study of factors affecting seed dispersai and survival are crucial to understanding the demographic and community dynamics of es. Seed dispersai may contribute to the growth and maintenance of local populations, maintain gene flux between populations, and permit plants to colonize a larger range of environmental niches (Bazzaz 1984, Denslow 1987, Louda 1989).

ln this study I will use two approaches to analyze factors affecting seed and seedling surv_ival. First, I will analyze and compare, at a small spatial scale, how variations in microenvironmental fact9rs affect seed and seedling survival of two common tree species in the Amazon forest Second, at a larger spatial scale, I will test the escape and colonization hypotheses (Janzen 1970, Howe and Smallwood 1982) by comparing seed survival near and far from parent trees, and between and within tree-fall gaps and the forest understory.

2-FACTORS AFFECTING POST-DISPERSAL SEED AND SEEDLING SURVIVAL IN TROPICAL FORESTS.

Natural tree regeneration in tropical forests is a dynamic and complex process. A combination of biological interactions and environmental factors at different scales of space and time affect the survival of seeds and seedlings, and generate pattems in the distribution and abundance of plant species.

Most mortality of tropical forest trees occurs during the pre- and post-gennination phases of the life cycle. During these phases, ecological interactions, such as seed and seedling predation, significantly affect plant reproductive performance by drastically reducing the survival of offspring (Janzen 1970,1971, Howe and Smallwood 1982, Clark and Clark 1984, Schupp 1989, Kitajima and Augspurger 1992). Therefore, an evaluation of the effects of the heterogeneous physical environment, together with the biological impact of seed dispersers and predators on seed and seedling survival, may reveal the processes governing the dynamics of tree populations and cornmunities at these initial stages.

Toe problem of scale is central in ecological theory and has been reviewed recently (see Levins 1992). Toe scales at which the interactions between seed dispersa! and predation occur and the environmental factors affecting them are important to consider. Available information indicates that seed and seedling survival can be affected differently over a broad range of scales.

Researchers have investigated seed survival of various plant species in relation to mortality factors acting at severa! scales. As yet, there has been no attempt to investigate seed survival of one plant species at a variety of spatial scales. Some informati.on exists Ón how seeds from different plant species are affected by microenvironmental factors such as leaf litter, (Molofsky and Augspurger 1991, Reader 1993), and variati.ons in gap size(Foster and Janson 1985). However, how a given plant species confronts many factors affecting seed survival at different spatial scales is not well explored.

To understand the mechanisms affecting tree recruitment, it is important to know whether tropical tree species with similar plant establishment requirements differ in their responses to a given miéroenvironmental factor (Lieberman et. ai. 1989). Some recent studies analyzed the effects of litter on survival of seeds according to their size and in relation to presence and quantity of leaf litter. They showed that tree species occupy a range of regeneration niches, because small-seeded species are more affected by litter than large-seeded species (Molofsky and Augspurger 1992, Reader 1993, Grubb 1977, Denslow 1987).

I speculated 'that different mortality factors would operate on different scales in the common, large-seeded palm, *Astrocaryum murumuru* and legume, *Dipteryx micrantha.* At scales of a few centimeters to lm, seed and seedling survival of these species could be affected by the presence and amount of leaf litter and understory vegetati.on cover (Shaw 1968, Harper 1977, Schupp 1989, Molofsky and Augspurger 1991). The effects of microenvironmental factors and spatial variations in the amount of leaf litter are explored in chapters 1 and 2.

At spatial scales of 10-20 m, seed and seedling survival may be affected by microhabitats or zones within gaps such as the crown and bole zone (Brandani et, al. 1988, Schupp 1988). At double this scale to 20-40m, seed survival could be affected by proximity to parent trees and density of parent trees (the escape hypothesis, Janzen 1970, Howe and Smallwood 1982, Wright 1983, Clark and Clar 1984, Howe 1991, Terborgh et.al.1991).

Parental effects on seed and seedling survival through negative distance and density effects (Janzen 1970, Howe and Smallwood 1982), are not necessarily independent of gap effects, because fruiting trees may be located inside or outside gaps. Therefore, parental effects on offspring survival should be tested in the sarne experiment investigating the effects of gftps. Few studies have included tree-fall gap and distance and density effects in the sarne experiment (but see Augspurger 1984, Schupp 1988, 1989).

Although density and distance effects on seed or seedling survival have been the focus of about 50 studies (e.g Janzen 1970, Howe and Smallwood 1982, Wright 1983, Clark and Clark 1984, Connell et.al.1991), the relative importance of these effects for individual trees remains controversial (see Janzen 1970, Connell 1971, Hubbell 1979, 1980, Howe 1991). ln their review on 25 studies on this matter Clark and Clark (1984) showed that half of the studies found density effects and the other half did not.

It is relatively common to find clumps of *Astrocaryum* and *Dipteryx* trees containing different numbers of trees and separated by up to 200 m from other clumps. Seed survival is possi?lY different under different-sized clumps of trees simply beéause areas with few trees may provide reduced local seed density and be less attractive to seed eaters than areas with high concentrations of seeds produced by large aggregations of adult trees.

A significant relationship between seed survival and the density of parent trees has been shown for *Astrocaryum mexicanum* in Mexico (Martinez-Ramos 1991). Although it is important for the understanding plant recruitment at population levei, such an analysis has not been attempted in the Amazon.

Severa! mechanisms operating at different scales may help to explain the high tree species diversity of tropical forests. Our ignorance of what determines spacing among individual conspecific trees in the tropics may be a consequence of the scarcity of studies at the population levei of frequency and density-dependent population regulation mechanisms and their associations with density-independent factors (Antonovics and Levin 1980). Therefore, more studies on seed and seedling dynamics need to be conducted in natural forests to strengthen the understanding of the processes affecting. the population and community dynamics of tropical tree species and the mechanisms that determine the spatial distribution pattems of trees in tropical forests. The effects of seed and seedling density, spacing of seedlings, distance from adult trees, and density of adult trees on *Astrocaryum* and *Dipteryx* seed and seedling survival is examined in chapter 3.

On still larger spatial scales, differences between forest habitats, such as gaps vs. understory may be important for progeny survival, due to the different physical conditions they present. For examp)e, fruiting *Astrocaryum* trees may be located near (<50m) or far (>100) from a gap. The effects of distance from a gap has not been investigated in the tropics.

Because gaps are produced by random events, they may be located at different distances from one another (in my study area, such distances varied between 50 and 200m). Toe spatial distribution of habitats and microsites within the forest, such as the contrast between treefall gaps and understory may be an important component of increased environmental heterogeneity at large scales (Colonization hypothesis, Augspurger 1984, Webb and Wilson 1985, Schupp 1989).

Finally, the importance of tree-fall gaps has been widely recognized in the regeneration of tropical rain forests (Grubb 1977, Hartshom 1978, 1980, Orians 1982, Denslow 1980, 1987, Bazzaz 1984, 1991, Horvitz and Schemske 1986, Farfan and Dirzo 1988, Uhl et.al. 1988, Brandani et.al. 1988, Schupp et. al.1988, Putz and Brokaw 1989, Garwood 1989, Clark 1991, Alvarez-Buylla and Garcia-Barrios 1991). However, few quantitative studies carried out in natural tropical forests, examined the establishment process on a range of spatial scales (Foster and Janson 1985, Wilson 1988, Schupp 1988, Rodriguez-Velasquez and Martinez-Ramos 1991, Molofsky and Augspurger 1992). ln chapter 4, I investigate the effects of gaps, gap size and distance from a gap on seed and seedling survival of ***Astrocaryum*** and ***Dipteryx.***

ln this study, I quantified natural leveis of seed and seedling survival and experimentally analyzed factors affecting the recruitment of two shade tolerant (sensu Whitmore 1984) amazonian forest trees, the palm ***Astrocaryum murumuru*** and the legume ***Dipteryx micrantha.*** I ran parallel experiments to investigate how the many of various environmental factors discussed above affect at different spatial scales the offspring survival of these two plant species.

Chapter 1

MICROSPATIAL HETEROGENEITY ANO THE RECRUITMENT OF TWO COMMON AMAZONIAN TREE SPECIES *Astrocaryum murumuru* (Mart.) and *Dipteryx micrantha*

Summary

I used naturally occurring variation in the properties of microsites to examine how several factors affect 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.* At small spatial scales, variation in leaf litter, understory vegetation, and incident light had significant effects only on *Astrocaryum* seed survival. Seedling growth and survival of both plant species were not affected by variations in the bioti.c and abiotic components of micro sites, such as microrelief, leaf litter thickness, presence of an adult tree, fungus attack on leaves, and herbivory. Survival of *Dipteryx* seedlings was inversely related to the number of plants of all species around them. At larger spatial scales (10 x 10 m^2 plots) *Astrocaryum* seedling survival was inversely related to the density of broad leafed monocots (*Heliconia* spp.), and positively related to incident light. The results of this study indicate that environmental heterogeneity created by leaf litter, understory vegetation, and light are important determinants of offspring survival in large-seeded tree species.

Introduction

Tropical forests are dynamic systems in which microsite mosaics are created by several types of small scale disturbances. Variati.ons in microrelief and edaphic conditi.ons are more predictable than localized conditions produced by spati.al and temporal variation of the leaf litter, light, density of understory herbs, density of seedlings, etc (Auerbach and Schmida 1987, and this study). Patterns in the distribution and abundance of plant species are ultimately determined by the number of seedlings that emerge from the soil, grow and survive (Janzen 1970, Harper 1977, Howe 1991). It is therefore important to investigate how seed survival and seedling growth and survival are influenced by a variety of micro environmental factors. Ultimately a better understanding of plant recruitment will illuminate the mechanisms underlying population dynamics, community structure and diversity (Ricklefs 1977, Grubb 1977, Hubbell and Poster 1990).

Seeds experience increased survival when they are transported away from the parent tree by dispersa! agents (Howe and Smallwood 1982, A gspurger 1983, Andersen 1989, Schupp 1988, Smythe 1989). However, dueto small to large scale gradients in abiotic and biotic factors on the forest floor, seeds and seedlings will encounter a range of conditions, some more conducive to survival than others (Augspurger 1984, Poster and Janson 1985, Denslow 1987, Molofsky andAugspurger 1992).

ln tropical forests, seed mortality often exceeds 70-90% (Janzen 1970, Howe et al. 1985, this study). Seed survival probabilities may depend strongly on the characteristics of the immediate environment, i.e, microrelief, density of leaf litter, vegetation cover, and incident light, as well as biotic factors such as seed density (Molovsky and Augspurger 1992, Denslow et al. 1991, Clark and Clark 1985, Howe et al. 1985). Conditions affecting seed survival also vary through time as shown in studies conducted in Panama which indicated that seed survival in a given microsite can not be predicted from year to year (Schupp 1989).

Harper et al. (1961) proposed the term 'safe site' to represent the properties of sites at which successful recruitment could occur. Studies of the factors which constitute a safe site (Harper 1977), and the distribution and frequency of safe sites have been conducted in temperate regions (Shaw and Antonovics 1986, Fowler 1988, Andersen 1989, Primack and Shili 1991). Despite their importance to tree regeneration, safe sites have not been very much investigated in the tropics.

While studying the Peruvian rain forest, I noted conspicuous differences in the spatial distribution of physical factors (light, microrelief, depth of litter, etc) and of biotic factors (vegetation cover, seed and seedling densities) around individual seeds and seedlings. I speculated that for the large-seeded and common tree species *Astrocaryum murumuru* and *Dipteryx micrantha,* factors acting on mortality would affect seeds and seedlings in different ways and at different spatial scales. Environmental heterogeneity at scales larger than the dimensions of an individual seed or seedling may become an important determinant of progeny performance (Auerbach and Schmida 1987).

Such effects can contribute to the fact that although these two plant species both have two-stage seed dispersai and share severa! seed and seedling predators, their population structures (plant size-distribution) are strikingly distinct (see results). Also seedlings of both plant species seem successful in low light (pers. obs.). However, tolerance to other microenvironmental factors, such as microrelief, amount of leaf litter, seed and seedling density, grazing, etc., may be equally or more important than available light depending on the circumstances (Connell and Slatyer 1977)

In this chapter, I focus on naturally-occurring variation in the properties of microsites, by investigating whether variation in microhabitat abiotic and biotic factors affect post dispersa! seed survival and the performance of established seedlings.

Microsite variation may be important for shade tolerant species because their seedlings have to persist in the poorly iluminated understory until a gap appears (Denslow 1980). Although ***Astrocaryum*** and ***Dipteryx*** offspring seem adapted to survive in the shaded understory, variation in the qualities of microhabitats must have effects on seed d seedling survival (Chazdon 1986, Marquis 1988).

For both plant species, I followed the fate of experimental seeds and monitored the survival of naturally dispersed ***Astrocaryum*** and ***Dipteryx*** seedlings, in small (lm^2 plots) and large areas (100 m^2 plots). I analyze the effects of various biotic and abiotic components of the microsites on seed and seedling performance.

Specifically, I investigated whether: (a) properties of the microsites affect seed survival, and seedling growth and survival, and whether (b) some of the sarne variables affect the survival of ***Astrocaryum*** seedlings at a larger spatial scales (plots of 100^2 m).

Metbods

STUDY AREA- I conducted the research at Cocha Cashu Biological Station (11° 54'S, 71 °19'W) in Manu National Park, Perú . Toe annual rainfall at C.C.B.S is about 2000 mm, and the mean annual temperature is approximately 24 °C. A single long dry season extends from May or June to October and altemates with a wet season which extends from November to April or May. Toe soil is a silty alluvium deposited by the Manu river (Salo et al. 1986). Toe forestis a mature moist tropical floodplain forest (Holdridge 1947, Terborgh 1983) containing many emergent trees and a characteristic complex vertical structure (Richards 1952, Terborgh and Petren 1991). Much information on the plant and animal communities of Cocha Cashu is available from 20 years of research (Gentry 1991).

BIOLOGY OF ***Astrocaryum murumuru*** and ***Dipteryx micrantha***

Hendersen (1994), in his recent book on palm species of the Amazon, adopts a new name for ***Astrocaryum macrocalyx***, which is ***Astrocaryum murumuru.*** This is the name I have used in this thesis. ***Astrocaryum murumuru*** is very abundant at Cocha Cashu, with population densities of up 30 adult trees/ha. Mature ***Astrocáryum*** attain heights of 18 to 20 m. This species is monoecious. Adults produce flowers during the wet season (December-January), and the fruits ripen in April-May. Toe fleshy sweet exocarp is avidly consumed by monkeys, especially capuchins. Discarded seeds are later eaten by peccaries and spiny rats, or are scatterhoarded and eaten by squirrels, agoutis, and other rodents. Trees produce one to three racemes of about 300 fruits each. Seed germination starts with the production of a small spiny (lateral) radicle. This initial phase persists for 1-2 months until the first leaf is produced. Seedlings possess 2-3 biphid leaves with white pubescent lower surface. Seedlings can be found around adult palms at densities of 1 to 5/m^2 (Table 1).

Dipteryx micrantha reproduces annually at Cocha Cashu. Mean height of adults was 44 m (N=32), although a few individuais reach 60 m. In contrast to ***Astrocaryum*** trees the typical density of ***Dipteryx*** is 2-6 adults/ha. Flowering takes place during November, after the rains have begun. Under just one tree I collected nearly 700 fruits for experiments. Some ***Dipteryx*** trees may produce more than 1000 fruits. Ripe fruits are dispersed by bats and then secondarily by rodents at the beginning of the following dry season (June). Germination begins in July and continues for 2 to 4 months, ending by late October. Germinating seeds remain 1 to 3 weeks with only the radicle emergent. Mammalian seed predators attack them heavily during this period. Subsequent growth of surviving seedlings to 20-30 cm height is fast and can occur within 1-2 weeks (pers.

observ.). Toe cotyledons are dropped within a few days after seedling emergence, leaving two compound leaves with 6 to 10 leaflets each. After the germination period, it is common to find adult trees surrounded by many seedlings at densities varying from 0.01 to0.56/m^2.

COLLECTING AND PREPARING EXPERIMENTAL SEEDS

I collected seeds along trails, from bat roosts, and beneath fruiting trees *(Astrocaryum* and *Dipteryx),* at least 1km from the experimental plots. Seeds were set out at experimental sites at the beginning of June, 1992. This was during the second week of the *Dipteryx* fruiting period, and about one month after *Astrocaryum* palms had dropped their fruits. Collected seeds were washed ln plastic basins and then dried for a few hours in the sun. Each seed was tested by floating, weighing, shaking and examining it for holes and scratches produced by seed predators. Only apparently viable seeds were used in the experiments.

Seeds used in the experiments were marked with a small letter "E" using a permanent marker pen, to differentiate them from naturally occurring seeds already present on the forest floor. Toe seeds were checked for survival weekly for 14 to 20 weeks, or until all the seeds at a site had been opened or removed by mammals.
I searched intensively once a week within a radius of 3-10 m, for seeds which had been displaced from the initial position. When possible, I removed the sarne number of naturally occurring seeds (those not marked or being used for experiments) from each experimental site in order to prevent an artificial increase in the local seed number as a result of the addition of experimental seeds. Few tree species were fruiting during the period of the experiment, so that keystone species, including *Astrocaryum* and *Dipteryx* were especially attractive to vertebrate consumers (ferborgh 1986).

Because the experiments were started during a period of food shortage, most of the seeds were probably not hoarded (Pers. Obs., but see Forget 1991). Infrequent hoarding was confirmed in a experiment in which about 300 seeds were distributed under fruiting trees. I glued small numbered magnets on the seeds and tracked them using a magnetic locator. I recovered most of the seed shells with the magnets. Up to 98% were eaten by seed predators. Most of the discarded seed coats were found near the experimental plots. Therefore, for the other experiments, seed disappearance was considered to be equivalent to seed predation.

To investigate how abiotic and biotic factors affect seedling growth and survival, I subdivided a 2.5 ha plot into 10 x 10 m subplots to map and tag all seedlings of both plant species and measured severa! factors from the microhabitat around each seedling (see further details in the next sections). I followed seedling performance of both plant species for three years (October 1991-October 1993).

EXPERIMENTAL DESIGN

FACI'ORS AFFECTING *Astrocaryum* and *Dipteryx* SEED SURVIVAL

Astrocaryum seeds- Experimental seeds were set out in five 10 x 10 m subplots distributed evenly along four 100 m parallel transects, for a total of twenty 10 x 10 m subplots. Seeds were arrayed evenly within $1 m^2$ subplots. Subplots were locatéd in each of the four comers of a 10 x 10 m plot. I used four different seed numbers (4, 8, 16, and 32) simulating the natural densities observed in the area.

Dipteryx seeds- A smaller number of seed sets was used in the corresponding experiment with *Dipteryx* , because the number of available seeds was limited. Toe design was the sarne as that used for *Astrocaryum* seeds, except that only ten 10 x 10 m subplots located in two parallel transects 20 m apart in the sarne 2.5 ha plot were used (Figure 1).

FACfORS AFFECTING *Astrocaryum* and *Dipteryx* SEEDLING SURVIVAL

Toe sarne 2.5 ha plot used for the seed set was also used to follow the performance of seedlings. I subdivided the plot in to subplots of 10 x 10 m. From October to November 1991, all seedlings of both *Dipteryx* and *Astrocaryum* found in the 250 subplots were mapped to the nearest 10 cm. A numbered aluminum tag was attached to each seedling in order to follow its subsequent growth and survival. In October 1991, I made severa! measurements, using simple techniques, around the seedlings of both plant species (see below).

Between October 1991 and September 1992, I revisited the plot five times to record growth and SQI'Vival of the seedlings. One additional survey was made in September 1993. Periodic censuses allowed me to distinguish mortality caused by fallen branches and fungus attack from mortality caused by seedling predators. A few seedlings were found covered by dead fallen branches, but still alive. I did not find evidence of seedlings being killed accidentally by fallen branches.

To investi.gate how micro- environmental factors might affect seedling growth and survival at a scale of a few centimeters, I measured and recorded seven environmental variables (see next section) within a radius of 20 cm around the seedlings, for 116 *Astrocaryum* and 190 *Dipteryx* seedlings, arnong those mapped in 1991. I also measured some of the sarne variables at the sites in which I placed experimental seeds in order to verify whether natural spatial variation in each variable could affect survival of *Astrocaryum andDipteryx* seeds.

FACTORS AFFECTING *Astrocaryum* and *Dipteryx* SEEDLING SURVIVAL AT A LARGER SPATIAL SCALES

To investigate how environmental variability might affect *Astrocaryum* seedling density, growth and survival at a scale one order of magnitude larger (in subplots of 10 x 10 m), I ran five parallel, 100 m long transects, 20 m apart, within a 1 ha plot nested in the sarne 2.5 ha plot. I recorded incident light, measured the thickness of the leaf litter layer, counted *Heliconia* and *Tectaria* plants (a common understory fern which can reach a half meter in height) and counted *Astrocaryum* seedlings in each 1 m^2 quadrant at the corners of the fifty 10 x 10 m subplots.

For environmental variables such as number of leaf litter layers, incident light, etc. (see next section) I repeated the measurements within each 1 m^2 quadrat"five times, taking one measurement at each comer and one at the center. Toe resulting values were used as an índex of each variable in models of multiple regression analysis.

RECORDING THE ENVIROMENTAL VARIABLES

LIGHT. Incident light was recorded five times (one at each corners and one at the center) in each of the 1m^2 subplots nested in the 10 x 10 m plot (see experimental design). Toe mean of these five measurements divided by a control value (see below), was the value used in the analysis. For seedlings, I measured incident light about five centimeters above each, and at the center and comers of twenty 10 x 10 m subplots, using an Extech light meter sensitive over a range of 0 to 50,000 lux. Incident light measurements were taken between 11:00 AM and 01:00 PM on completely overcast days to avoid direct light. To obtain a relative scale each value was divided by a control yalue

(mean of measurements taken during the sarne ·period at the center of a lake located about 1km from the 2.5 ha plot)

MICRORELIEF. Small differences in microrelief may be associated with differences in soil moisture and compaction. During dry periods moisture may promote seedling survival, and local differences in soil compaction may be important in determining where seedlings will successfully establish. Two types of microrelief representing obvious edaphic differences were distinguished: (a) low, consisting of circular depressions, where water accumulates after heavy rain during the wet season and characterized by little or no leaf litter cover, and (b) high, consisting of the normal leve! of surface of the forest floor which is covered by leaf litter and seldom flooded.

LEAF LITI'ER- To record leaf litter cover, I used a 1 m^2 PVC frame (subdivided into 25 x 25 cm squares), which I placed at *50* cm height above each experimental 1 m^2 subplot with seeds, and counted the number of 25 x 25 cm subdivisions covered by leaf litter. I then divided the number of squares covered by litter by the total number of squares (25) to obtain the litter cover index (LCI), or the proportion of the area covered by leaf litter. I also measured the number of leaf litter layers at each comer of the PVC frame.

Leaves fell continually during the period of the experiment (about *5* months). The number of leaf litter layers recorded was therefore subject to change. I considered the variance produced by this temporal effect. I averaged the litter values obtained during four monthly measures. These values were used as the leaf litter layer index (LLL).

For the seed and seedling part of the study, I measured the depth of the litter layer by forcing a wire with a hooked tip through the litter and counting the number of leaves it perforated. For some models in the data analysis, I scored the number of leaf litter layers as a caterigorical variable (low=O to 2; medium=3 to *5;* high=6 to 9 leaf layers).
I measure litter layers because other important factors, such as light, temperature,

moisture and nutrient availability, have shown increasing variability as the amount of litter increases (Facelli and Pickett 1991, Molofsky and Augspurger 1992).

PRESENCE, DENSITY AND COVER OF UNDERSTORY VEGETATION- For the seed experiment, I used a 1 m^2 PVC frame (subdivided into 25 x 25 cm squares) which I placed 50 cm above each experimental 1 m^2 subplot with seeds, and counted the number of 25 x 25 cm subdivisions covered by broad-leafed monocots "platanillo" *(Heliconia* spp.), or ferns *(Tectaria* spp.), and the total cover- of ali other plants species present, including these two. I divided the number of squares representing each of these cover types by the total number of squares (25) to obtain the relative area covered by each, and designated them, respectively, as the *Heliconia* cover index (HCI), *Tectaria* cover index (TCI), and total vegetation cover index (TVC).

For each *Dipteryx* and *Astrocaryum* seedling mapped and measured, I recorded whether it was under a "platanillo" *(Heliconia* spp.), a fem (*Tectaria* spp.), or neither. In addition I estimated the local density of *Heliconia* and *Tectaria* by counting the number of individuais in each of the four 1m^2 subplots located at the comers of the twenty five 10 m x 10 m subplots. I also recorded the number of understory plants of all other species (up to 30 cm height) in an area of 20 cm around each experimental seedling. Toe importance of other competing plants for seedling growth and survival has been emphasized by Harper (1977), and in some recent studies in tropical forest (Rankin 1978, Denslow et al. 1991). Preliminary observations clearly indicated that shading by the large, horizontal leaves of *Heliconia* affected the number of new leaves *Dipteryx* (and probably *Astrocaryum)* seedlings produce in the first year after establishment. *Dipteryx* seedlings under *Heliconia* plants did not produce new leaves, whereas seedlings in the sarne site not located under *Heliconia* plants sprouted at least one new leaf.

HERBIVORY. I used a qualitative assessment, presence or absence of herbivory. Seedlings showing any leaf damage were scored as having been attacked by herbivores.

THE RESPONSE VARIABLES

SEED SURVIVAL. For seed survival, I first compared whole survival curves, and the associated covariates, measured at the microsites with respect to the four seed densities (treatments). I also compared the number of weeks until 50% of the experimental seeds had disappeared. I used time to 50% survivorship because, seed predators may be attracted to different-sized aggregations of seeds. Initial conditions therefore may be important.

SEEDLING GROWTH. *Astrocaryum* seedlings do not produce a stem for severa! years, but only leaves, As an índex of seedling growth, I used the number of leave produced: GIDX (growth índex) = FNL (final number of leaves) - INL (initial number of leaves). For *Dipteryx* seedlings, I measured height growth.The following growth index was used: GIDX= Gf (final seedling height (cm) after one year) - Gi (initial seedling height after its emergence from the soil).

SEEDLING SURVIVAL. For both plant species seedling survival was used in the analysis as a binary variable, i.e seedling survived (=O) or died (=1). See next section.

STATISTICAL ANALYSIS.

For the seed experiments, I used two statistical approaches. First, to investigate the effects of microsite features (covariates) on seed survival, I used survival analysis, fitting a Cox proportional hazard model available in Splus to seed survival data curves. This analysis is a binomial log-log regression that combines all censuses into a single test, correctly encompassing right-censored data, i.e. seeds persisting ative until the end of the experiment for which survival times are unknown. The Cox pr<?cedure calculates a "survival function", which represents the proportion of the initial seed population still present at each weekly census. In a complementary analysis, I used both the Mantel-Haenzel test (Log-Rank test), and Peto-Peto's test (a modification of the Gehan-Wilcoxon test) (Splus 1991) to compare survival functions across seed density treatments, since the former test weights longer survival while the latter test emphasizes early survival (Splus 1991).

Analysis of variance (Two-way ANOVA) was used to investigate whether the response variable "time at 50% seed survivorship (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 microsites variables. I used multiple regression analysis to assess whether time to 50% seed survivorship for eac plant species was affected by leaf litter, vegetation cover, and seed density.

To analyse seedling performance, multiple regression analysis (MGLH Systat procedure, Wilkinson 1991) was used to investigate whether biotic and abiotic features of the microsites around the seedlings affected seedling growth. I used also logistic regression analysis (SAS 1987), to investigate how microsites features affected seedling survival in both plant species. In these models, the response variable was binary, i.e., whether seedlings survived (=0) or died (=1) one year after tagging. Responses were analyzed in relation to such factors as microrelief, litter layer, vegetation cover, incident light and seedling growth. Logistic regression analyses the determinants of a categorical response variable. In principie, logistic regression is more appropiate than multiple regression in analyses in which the response variable is binary. Seedling growth and numbers surviving were analyzed on a scale of 10 x 10 m subplots using multiple regression models (MGLH Systat procedure, Wilkinson 1991) to identify the effects of various factors.

Results

Astrocarym murumuru and *Dipteryx micrantha* at Cocha Cashu are similar in the season they produce fruits, in the size of fruits, seeds and seedlings, and in the secondary seed dispersors and predators (Table .1). Despite these many similarities they have different plant size population structure within the 2.5 ha plot I studied. *Astrocaryum's* population in the area presents abundant individuais in all class ages: (1) 15% of seedlings - plants with one to two leave.s and smaller than 30 cm in heigth; (2) 68% of juveniles 1- plants with three to six leaves and 31-120 cm in height; (3) 12% of juveniles 3- plants with six to nine leaves and 121-250 cm in height; (4) 2% of sub-adult plants with nine to twelve leaves and 251-450 cm, and (5) 3% of adults- trees with 450 cm or higher.

Dipteryx population presents: (1) 33% of seedlings- plants with two leaves and less than 30 cm in height; (2) 58% of juveniles-plants with 31-120 cm in height; (3) 7.0% of saplings - plants with 121-250 cm in height; (4) and 2.0% of adults- large trees which reach up to 60 m in height

EFFECTS OF SPATIAL VARIATION OF LEAF LIITER , VEGETATION COVER AND SEED DENSITY ON *Astrocaryum* and *Dipteryx* SEED SURVIVAL

In the seed experiment only 108 (9%) of 1200 *Astrocaryum* seeds survived after 20 weeks, and 32 (5 %) of 600 *Dipteryx* seeds survived after 14 weeks.

Most of the environmental variables measured at the experimental microsites where ***Astrocarywn*** experimental seeds were sown, sho\\:'ed no strong correlation arnong them (Table 2). To decide which variables I should use in the statistkal analysis I adopt the following criteria: In the Pearson correlations matrix results (Tables 2 and 5), those variables presenting correlation coefficient values lower than 0.50 with any other variable were the ones used in the analysis. For exarnple, Total Vegetation Cover (TVC) had relatively high correlation with ***Heliconia*** cover index (HCI). Toe sarne was true between Leaf Litter Layer (LLL) and Leaf Litter Depth (LLD). Therefore these variables ((TVC, HCI) and (LLL, LLD)) were not included together as independent variables in any statistical analysis in this study.

Results from fitting Cox models to swvival curves considering the covariates mentioned above, suggest that the survivai of ***Astrocarywn*** seeds was enhanced at microsites with relatively higher leaf litter cover and vegetation, and also in better iluminated sites (Table 3). This indicates that some sites in the forest are safer than others for ***Astrocarywn*** seeds, because mammal seed predators do not find the seeds at the sarne rate everywhere. However the sarne seed predators seem to respond to variation in seed number because ***Astrocarywn*** seed survival was negatively density-dependent (Table 3).

Although the ***Dipteryx*** seeds were sown in the sarne 2.5 ha plot with ***Astrocarywn*** seeds, their survival was not affected by spatial variation in any microsite factors (Table 3). The odor of ***Dipteryx*** seeds is much stronger than that of ***Astrocarywn*** seeds and may facilitate their location by mammalian predators.

There were no significant differences between the two plant species in the number of weeks to 50% survival at the four seed densities (4, 8, 16, and 32). However, there was a highly significant difference in long term seed survival between the two plant species, with no interaction between seed density and plant species. (Table 4, and Figures 2 and 3).

For both *Astrocaryum* and *Dipteryx*, spatial variation in leaf litter cover and thickness, and variation in two types of vegetation cover *(Heliconia* and *Teclaria)* had no significant effects on the time to 50% seed survival (Multi.pie regression analysis for *Astrocaryum*, r^2=0.09, df=73, n=80, p>0.05; for *Dipteryx*, r^2=0.129, F=0.817, df=33, n=40, p=0.564). *Astrocaryum* seed density significantly influenced *Astrocaryum* seed survival, with seeds surviving longer at microsites with more seeds (coefficient for the partials from the sarne multi.pie regression = 0.025, T=2.40, p<0.05).

SEEDLING SURVIVAL IN THE 2.5 ha PLOT. One year after germination, *Astrocaryum* seedlings had experienced relatively lower mortality (7%) than *Dipteryx* seedlings (39%). Most of the seedling mortality was due to predation by mammalian herbivores, probably deer and Paca, which are relatively common in the area. A few seedlings (< 1%) of both plant species died from fungus attack. Types of evidence used to indicate predation by vertebrates were: seedlings cut at the stein base, seedling and attached seed removed completely from the ground *(Astrocaryum)*, or seedlings absent from the site where they had been mapped and tagged.

EFFECTS OFMICRORELIEF, LEAFLITIER, UNDERSTORY VEGETATION, PATHOGENS, ANO LEAF HERBIVORY ON SEEDLING GROWTH ANO SURVIVAL OF *Astrocaryum* and *Dipteryx*-

Astrocaryum seedlings- There were weak correlations among the seven variables, measured at the microsites where *Astrocaryum* seedlings established: microrelief, number of leaf litter layers, abundance of nearby understory plants, presence of adult palm trees, presence of fungi on seedling leaves, evidence of herbivory, seedling growth (Table 5). Therefore, except for the presence of fungus on seedling leaves, for which the sample size was small, I used the remaining variables in multiple regression and logistic regression models to investigate their relative contributions to variance in the two response variables: *Astrocaryum* seedling growth and survival.

None of the factors significantly affected *Astrocaryum* seedling growth (Multiple regression analysis, r^2=0.063; n=61; F=0.743; p=0.594). Moreover, the survival of *Astrocaryum* seedlings after one year, was not significantly affected by any of these factors (fable 6).

Two variables, the presence of platanillos *(Heliconia* spp.) and incident light, were used in separate models for *Astrocaryum* seedling survival. This was due to the small number of cases of both variables relative to the other six variables used. Also because the sample size was small for light at individual *Astrocaryum* seedlings, this was the only variable not used in the model analysing *Astrocaryum* seedling performance, although it was considered for *Dipteryx* seedlings. Neither seedling growth nor shading by *Heliconia* herbs *affectedAstrocaryum* seedling survival (Logistic regression for growth, x2 p-value =0.269, Wald test x2 =1.220, N=61; for *Heliconia* shadding effects, x2 p-value = 0.719, Wald test x2 =0.129, N=l 15)

Dipteryx seedlings. There were no strong correlations (Table 5) among the eight microenviromental variables used in the models for analysing the survival of *Dipteryx* seedlings (microrelief, thickness of leaf litter layer, abundance of nearby understory plants, presence of *Heliconia* spp., seedling herbivory, presence of fungus on the seedling leaf surfaces, seedling growth, and incident light).

I included seedling growth in the correlation matrix because it was used as an independent variable in some models. I again ran a multiple regression analysis with this variable in the sarne way I did for *Astrocaryum* seedlings. *Dipteryx* seedling grow did not correlate with any of these variables (r2=0.068; N=82; F=0.453; p=0.479). Among all of these factors, only the number of woody plants around *Dipteryx* seedlings had significant effects on *Dipteryx* seedling survival (Table 6).

For *Dipteryx* seedlings, I recorded two additional variables (incident light and *Heliconia* cover). These two variables were used in a different model, together with *Dipteryx* seedling growth, to investigate their effects on *Dipteryx* seedling survival. Shading produced by the large-leafed *Heliconia* herbs did not affect *Dipteryx* seedling survival (Logistic regression, x^2 p-value =0.552, Wald test x^2 =0.353, N=105). However both incident light and *Dipteryx* seedling growth had significant effects on *Dipteryx* seedling survival (Logistic regression, for incident light x^2 p-value= 0.051, Wald test x^2 =3.818, N=105; for growth index x^2 p-value= 0.013, Wald test x^2 =6.0982, N=105). *Dipteryx* seedlings located in better illuminated microsites were more vulnerable to grazing by herbivores than those in shady sites in the understory. Also, seedlings that grew faster suffered more predation by vertebrate herbivores.

EFFECTS OF LEAFLI'ITER, UNDERSTORY VEGETATION, *Astrocaryum* SEEDLING DENSITY AND INCIDENT LIGHT ON *Astrocaryum* SEEDLING GROWTH AND SURVNAL ON LARGER SPATIAL SCALE

I was not able to analyze *Dipteryx* seedling growth and survival on the scale of 10 x 10 m subplots because of the small number of replicates. At this scale the correlations among independent variables were not strong (Table 7). On this ten fold larger scale, none of the independent variables (mean leaf litter tickness, mean *Heliconia* density, mean *Tectaria* density, *Astrocaryum* seedling density and mean incident light) had significant effects on *Astrocaryum* seedling growth (Multiple regression analysis, r2= 0.171; N=19; F=0.537; p=0745). However, three of these variables (mean *Heliconia* density, mean incident light and *Astrocaryum* seedling density) had significant effects on *Astrocaryum* seedling survival. These results suggest that a higher number of *Astrocaryum* seedlings survived in more shaded sites, and also in sites with higher densities of seedlings and *Heliconia* herbs (Table 8 and Figure 4).

Discussion and conclusions

Toe 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 (Harper 1977). Small seeds, such as those from most pioneer species, tend to remain in dormancy until conditions for germination arise (Garwood 1989). Small seeds are also rapidly incorporated into the soil seed bank, which makes them less vulnerable to seed predators. Because they are more easily detected, large seeds, such as those of *Astrocaryum* and *Dipteryx*, may be exposed to strong predation pressure by mammalian seed-eaters (Janzen 1970, Smythe 1989, Forget 1993, Terborgh et al. 1993).

Few studies in the tropics have investigated how a given microenvironmental factor, alone or in conjunction with other factors, and operatjng at different spatial scales, affects seed and seedling performance (see Schupp 1989, Denslow et al. 1991, Molovksky and Augspurger 1992). In addition to identifying biologically significant microenvironmental factors, it is also important to determine the circumstances in which any particular factor affects survival. Moreover, the scale at which such factors affect seed and seedling survival may depend on the plant species in question and the properties of the macro and microenvironment where propagules establish. For example, variation in the size and interna! structure of tree-fall gaps, and also the spatial distribution of understory vegetation (microhabitats), have been demonstrated to affect seed and. seedling survival (Denslow 1980, Brokaw 1987, Schupp 1989, Denslow et al. 1991).

The results of this study indicate that at small spatial scales various abiotic and biotic factors such as leaf litter, vegetation cover, and degree of openess (determined as the amount of incident light) affected only *Astrocaryum* seed survival. *Astrocaryum* and*Dipteryx* seeds had different chances of survival in similar microsites. This suggests the possibility of some niche partioning in space by the two plant species. lnitial difference at recruitment may have consequences for seedling competion between the two species. Some microsites were safer than others for *Astrocaryum* seeds, but not for *Dipteryx* seeds. This may create s_ome advantanges for *Astrocaryum* at the initial stages of populational recruitment. If most of the seeds germinate, a higher number of *Astrocaryum* seedlings would be expected to occur in the ar a. In fact, the number of *Astrocaryum* seedlings in the area is at least tive times that of *Dipteryx* seedlings. But this could also be just because *Astrocaryum* has five times more adult trees than *Dipteryx*.

At the level of plant c mmunity, the mosaic of microhabitats in the study area may creates opportunities for specialization, which, in tum, promote local diversity. The seeds respond mostly to current conditions, so natural selection probably has resulted in each plant species responding to a combination of factors for germination, which may be followed by another combination of factors favourable for seedling establishment (Fenner 1985). Although this correlation between pre-germina on and post-germination conditions can never be complete, it should have high probability otherwise plant would not be able to exploit it (Fenner 1985).

The results also suggest that predation by animais is a critica! factor affecting seed and seedling survival of these two plant species. Few seeds survived to the end of this study. Apparently, there are few safe microsites for large seeds to survive in this forest

High vulnerability to seed predators may be a consequence of large seed size. Less than 10% of all seeds of both species used were alive at the end of the experiment (or after only 20 weeks has passeei), due to high seed predation by mammals.

No matter where ***Astrocaryum*** or ***Dipteryx*** seeds land on the forest floor, vertebrate seed predators, such as the spiny rat, agouti, squirrels, and peccaries will find them. Effeciency in finding large seeds may be facilitated by seed size itself, and also by seed-predator competition during periods of food scarcity. Furthermore, seed predators may forage preferentially in different sites (Price and Jenkins 1986, Emmons 1982). Predators' success in finding seeds may depend upon the physical characteristics of the microsite. Both open illuminated and more closed microsites (with more litter and vegetation) were conducive to ***Astrocaryum*** seed survival. This may have resulted from the activities of more than one kind of seed predator. For example, small and medium sized-rodents, such as spiny rats and agoutis, concentrate their foraging in small areas, and may scan the area in a fine-grained search. Peccaries in contrast, cover much larger arcas and may forage in a coarse-grained fashion. Moreover, differences in the way nocturnal and diurna! seed predators search the environment could be important to defining safe sites. To nocturnal predators, illumination of sites may-be not important, while these factors míght help diurna! seed predators to find their food.

Although ***Astrocaryum*** and ***Dipteryx*** seeds have similar size, their morphologies differ. ***Dipteryx*** seeds possessa thick, hard pericarp. During the pre-germination period, ***Dipteryx*** seeds may be vulnerable only to animals with strong jaws and adapted teeth such as squirrels and other rodents (Kiltie 1981). However, during the dry season, ***Dipteryx*** seeds desiccate and are much easier to open, because the two pericarp valves separate. That also happens a few days before they germinate. ***Dipteryx*** seeds then become very vulnerable to a wide range of potential mammalian herbivores (Terborgh Pers. Com.). Toe germination phase therefore, may be a critica! phase in the establishment of ***Dipteryx.*** Seeds-that germinate and pass on to the seedling stage will have better chances for survival, because of a reduced number of seedling predators relative to seed predators (Janson and Emmons 1990). Also primary ***Dipteryx*** seed dispersa! by bats may help to minimize the impact of seed predators near the parent tree by satiating them at bat roost sites located farther from adult trees.

Astrocaryum germinating seeds are less atractive to seed eaters because the radicle and the first stem are spiny. Therefore, the crucial phase in the early establishment of this species is during the pre-germination phase, when many mammal and some insect species (bruchid beetles) rely on them.

Toe results of this study support the observation that seedlings that emerge from large seeds are less affected by variations in externa! environmental factors than those which germinate from small seeds (Harper 1977). Both ***Astrocaryum*** and ***Dipteryx*** have similar seed size and similar secondary seed dispersers (Table 1). ***Astrocaryum*** seedlings could be characterized as shade tolerant (sensu Swaine and Witmore 1988), because they survive in the poor light environment of the understory until a tree fall gap is formed nearby. ***Dipteryx*** seedlings seem to be more light demanding and gap opportunists (Clark and Clark 1985). Toe results for the seed part of the study provide little support for the idea that ***Astrocaryum*** and ***Dipteryx*** may possess similar needs for regeneration niches.

Dipteryx seedlings that grew faster and reached larger sizes were more heavily attacked by herbivores. Similarly De Steven (1991a,b) found more browsing by deer on ali six plant species that produce larger seedlings at her experimental site near the Eno River in North Carolina.

The second topic addressed in this chapter was the spatial scale at which physical and biotic factors may influence offspring performance. Toe survival of ***Astrocaryum*** seedlings was dependent on spatial scales larger th those of the microsites around a given plant (results from the 10 x 10 m plots). This indicates that offspring survival may be related to the spatial scales in which the seed and seedling predators operate, a result also found for ***Dipteryxpanamensis*** in Costa Rica (Clark and Clark 1984, 1987, see also chapter 3).

ln this study, seed and seedling survival probabilities were found to be a function of severa! factors acting at larger scales such as: 1- seedling density, 2- variation of incident light, 3- the density of the vegetation cover produced by other plant species in a patch of forest. A high density of understory herbs can increase shading and competion for light and nutrients, and may also reduce detection by seed predators (Denslow et al. 1991, De Steven 1991a). ln a Costa Rican rain forest, the results of Denslow et al. (1991) suggested that large-leafed understory plants compete with seedlings of canopy trees by reducing the already limited light (2 % of full sun light). These authors suggested that small differences in incident light could significantly affect the growth and survival of plants growing at light levels close to their photosynthetic compensation point.

: Toe fact that fewer ***Astrocaryum*** seedlings survived in better illuminated spots reflects a possible preference of mammal seedling predators for well-illuminated foraging sites (Price and Jenkins 1986). Recently emerged seedlings bear soft and nutrient -rich leaves. At Cocha Cashu, deer forage in small, well-illuminated gaps (Pers. Obs.), pehaps because of the higher probability of finding recently established seedlings than in the dark understory. ***Astrocaryum*** seedling survival in 10 x 10 m plots was higher in plots containing higher ***Astrocaryum*** seedling densiti_es, which suggests that predators may have been satiated (Janzen 1970), and that some sites may be more appropiate for· establishment than others. Also it could indicate that the best conditions for ***Astrocaryum*** seedlings are marked by the presence of seedlings that established on previous years.

Although insects and fungi damaged the leaves of many ***Astrocaryum*** and ***Dipteryx*** seedlings, mammals that consumed the entire seedling were the main cause of mortality. Toe ability of ***Astrocaryum*** and ***Dipteryx*** seedlings to recover after herbivory and fungus attack may be limited especially for seedlings located in poor light environments (see Augspurger 1984, and Clark and Clark 1985).

Toe degree to which the damage caused by insects and fungi affected seedling growth is difficult to assess because variations in microenvironmental factors , such as leaf litter, humidity, light, temperature, vegetation and localized air currents could be important for the dispersion of pathogens and insects. Interactions among these factors makes it difficult to understand what determines pattems of damage produced by insects and fungi (Denslow et al. 1991).

Periodic inundations produced by long rainy periods or ri.ver flooding could be another factor affecting the likelihood of establishment of seedlings at the Cocha Cashu forest on a large scale. Toe most elevated portions of the floodplian have been flooded once in the last 25 years. Most of the rainfall at Cocha Cashu occurs between November and arch. Although flooding does not persist for some months, pools of rain water do, and this may limit the number of seedlings that can establish in the area. However, for both *Astrocaryum* and *Dipteryx* , seed drop and dispersa! occur soon after the end of the rainy season (in March). Because most *Dipteryx* seeds germinate at the end of the dry season (October- November), they may escape long periods of flooding which are likely to be more frequent during the wet season. *Astrocaryum* seeds apparently experience greater variation in the duration of seed dormancy (pers. obs.), therefore seedlings may be established at any time in the area. This property combined with the large number of seeds produced and high density of adult trees may partially explain the abundant regeneration of this palm tree in the area.

ln conclusion, the results suggest that the recruitment pattems of both tree species depend on biotic and abiotic factors. Toe most important of these are high post-dispersal seed predation and the properties of microsites. The relative importance of these effects differs for the two plant species.

Finally, recruitment of *Astrocaryum and Dipteryx* is affected in different ways by the environmental heterogeneity created by litter, vegetation and light at different spatial scales. Resistance to externa! circumstances may be conferred by seed reserves. However, in subsequent years, seedling performance must result from the ability of seedlings to modify soil physical and chemical conditions, and also by changing through growth their imediate light environment in the microhabitat. Apparently more ***Astrocaryum*** seeds pass intact through the critica! period (dry season or when most of the vertebrates rely on them for food supply). ***Astrocaryum*** may experience greater recruitment than ***Dipteryx*** simply because of the much greater number of seedlings produced every year. To better understand the effects of abioti and biotic properties of microsites it would be necessary to experimentally transplant seedlings to different microhabitats. This would allow the assessment of seedlings' ability to change their microenvironment and how the subsequent changes in microsite components affect future seedling performance and the frequency of recruitment of both plant species.

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Table 1. Comparison of some characteristics of ***Dipteryx micrantha*** (Leg.) and ***Astrocarium murumuru*** (Palm) recruitment pattems in Cocha Cashu.

	Dipteryx	***Astrocarium***
Phenol0&):	Annual	Annual
Fruiting period	June-August	March-April
Type	Drupe, smooth	Drupe, spiny
Color	Green	Orange
Fruitcrop	100 to >1000	100 to> 500
Fruit size (cm)	3.3-6.4x2.0-4.0x1.7-3.3 (n=ll)	4.7-6.6x2.0-2.8 (n=15)
Pulp width (mm)	3.25 ± 0.23 (n=6)	3.16 ± 0.87 (n=15)
Fruit weight (g)	27.5 ± 1.40 (15-43; n=24)	15.5 ± 2.43 (12-19; n=15)
Seeds		
Size (cm)	3.0-6.0xl.8-3.8xl.5-3.0 (n=22)	2.7-4.8x2.2-2.8xl.6-2.4(n=10)
Weight (g)	21.5 ± 2.92 (8-40; n=ll)	7.4 ± 1.08 (5.4-8.9; n=l 1)
Seed Dis.persaJ		
Syndrome	zoochory	zoochory
Primary agents	Bats, monkeys, macaws	Squirrels, monkeys
Distance	1 to >500 m	0.10 to <30m
Secondary agents	Agoutis, spiny rats, squirrels	Agoutis, spiny rats, squirrels
Distance	1 to >20m	1 to >20m
Germination	September-December	September-December
,S.eed Predators		
Arboreal	Macaws, monkeys, squirrel	Monkeys, squirrels, insects
Terrestrial	Agoutis, spiny rats, squirrels	Agoutis, rats, squirrels,
insects		
Seedlin&s		
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)
Stern diameter (mm)	3.7±2.67(2.7-4.3; n=31)	-
Adults		
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.

Table 2. Pearson Coqelation matrix for the factors measured near *Astrocaryum* experimental seeds (groups of 4, 8, 16 and 32; n=80 seed groups) and *Dipteryx* experimental seeds (groups of 4, 8, 16 and 32; n=40 groups). Leaf Litter Cover Index (LLC), Leaf Litter Depth (cm) (LLD), number of Leaf Litter Layers (LLL), *Heliconia* Cover Index (HCI), *Tectaria* Cover Index(TCI), Total Vegetation Cover Index (TVÇ), and Light Index (LIG).

	LLC	LLD	LLL	•HCI	TCI	TVC	LIG
Astrocaryum							
LLC	.						
LLD	0.316 (0.004)	.					
LLL	0.401 (0.000)	0.914 (0.000)	.				
HCI	0.058 (0.607)	-0.078 (0.490)	-0.019 (0.864)	.			
TCI	-0.058 (0.607)	0.047 (0.680)	-0.080 (0.478)	-0.251 (0.025)	.		
TVC	0.033 (0.771)	0.055 (0.627)	-0.002 (0.988)	0.544 (0.000)	0.332 (0.003)	.	
LIG	0.088 (0.438)	-0.213 (0.058)	-0.121 (0.284)	0.026 (0.821)	-0.157 (0.164)	0.069 (0.541)	.
Dipteryx							
LLC	.						
LLD	0.357 (0.024)	.					
LLL	0.379 (0.016)	0.851 (0.000)	.				
HCI	0.206 (0.203)	0.265 (0.098)	0.045 (0.781)	.			
TCI	0.248 (0.122)	0.146 (0.370)	0.193 (0.232)	-0.311 (0.051)	.		
TVC	0.503 (0.001)	0.471 (0.002)	0.334 (0.035)	0.364 (0.021)	0.507 (0.001)	.	
LIG	-0.047 (0.771)	-0.243 (0.131)	-0.171 (0.291)	0.061 (0.710)	-0.242 (0.132)	-0.301 (0.060)	.

Numbers within parenthesis are p-values for the corresponding correlation coefficients; For *Astrocaryum,* Bartlet Chi-square statistics=241.63, DF=21 p=.000; For *Dipteryx,* Bartlet Chi-square= 114.01, DF= 21 , p=0.000

Table 3. Survival of *Astrocarywn* and *Dipteryx* seeds in relation to various environmental variables (covariates), components of the microsites where the seeds were placed (Cox Proportional Hazard Regression).

Parameter	DF	Estimates (SE)	Z	Sig. level
Astrocarywn +				
Heliconia	6	-0.019 (0.186)	-0.102	ns
Tectaria	6	0.286 (0.234)	1.218	*
Litter cover	6	1.963 (0.432)	4.540	***
Litter layer	6	-0.247 (0.046)	-5.367	***
Lightindex	6	1.147 (0.231)	4.966	***
Seed density	6	-0.016 (0.003)	-5.370	***
Dipteryx++				
Heliconia	6	-0.434 (0.865)	-0.502	ns
Tectaria	6	-0.807 (0.624)	-1.293	ns
Litter cover	6	-0.222 (0.188)	-1.180	ns
Litter layer	6	0.017 (0.644)	0.261	ns
Lightindex	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 on 6 DF, $p<0.0001$;
++ Likelihood ratio test=11.5 on 6 DF, $p<0.0739$

Table 4. Results of two-way Analysis of Variance (ANOVA) of the response variables number of weeks to 50% seed survival of ***Astrocaryum*** and ***Dipteryx*** seeds, on categorical variables "seed number" (four seed number treatments) and "plant species" (***Astrocaryum*** and ***Dipteryx***).

Source of Variation	SS	DF	MS	F
Seed number	42.317	3	14.106	0.873ns
Species	170.017	1	170.017	10.523***
Seed number"'species	65.250	3	21.750	1.346ns
Error	1809.500	112	16.156	

ns=not significant; ***= p=0.001

Table 5. Pearson Correlation Matrix of factors measured at microsites near *Astrocaryum* (n=61) and *Dipteryx* seedlings (n=83). MICRORELIEF (MIC), LEAF LITTER LAYER (LLL), abundance of all other plants within 20 cm radias of *Astrocaryum* and *Dipteryx* seedlings (ABO), presence of adult palms of any species shading the seedlings (UNP), presence of *Heliconia* herbs shading the seedlings (HEL), presence of fungi (PA1) on the seedling surface, evidence'bf herbivory (damage to seedling leaf surface) (HEB) and seedling growth over one year (GWT).

Astrocaryum

	MIC	LLL	ABO	UNP	PAT	HEB	GWT
MIC	.						
LLL	0.126 (0.332)	.					
ABO	-0.257 (0.045)	0.083 (0523)	.				
UNP	0.252 (0.050)	-0.203 (0.116)	-0.125 (0.336)	.			
PAT	-0.033 (0.798)	0.002 (0.990)	0.007 (0.957)	-0.208 (0.107)	.		
HEB	-0.011 (0.932)	-0.013 (0.919)	0.023 (0.862)	0.026 (0.844)	-0.362 (0.004)	.	
GWT	0.152 (0.242)	0.182 (0.161)	-0.032 (0.806)	0.108 (0.407)	0.000 (0.997)	-0.004 (0.977)	.

Dipteryx

	MIC	LLL	ABO	HEL	HEB	PAT	GWT	LIG
MIC	.							
LLL	0.303 (0.005)	.						
ABO	0.239 (0.029)	0.026 (0.817)	.					
HEL	-0.262 (0.017)	-0.190 (0.085)	0.025 (0.825)	.				
HEB	0.158 (0.154)	-0.076 (0.497)	0.068 (0.539)	-0.219 (0.047)	.			
PAT	-0.261 (0.017)	-0.214 (0.052)	-0.198 (0.072)	-0.014 (0.899)	0.079 (0.477)	.		
GWT	-0.017 (0.882)	-0.156 (0.159)	.0.010 (0.930)	0.114 (0.305)	-0.047 (0.670)	0.165 (0.136)	.	
LIG	0.181 (0.102)	0.143 (0.196)	0.028 (0.803)	-0.036 (0.747)	-0.148 (0.181)	0.057 (0.612)	0.182 (0.099)	.

Numbers within parenthesis are p-values for the corresponding correlation coefficients; For *Astrocaryum,* Bartlet, Chi-square statistics=27.67, DF=21 p=.150; For *Dipteryx,* Bartlet Chi-square= 52.35, DF= 28, p=0.003

Table 6. Results of logisti.c regression analysis of the response variables, *"Astrocaryum* and *Dipteryx* seedling survival" on the variables: MICRORELIEF (low and high ground), LEAF LITfER THICKNESS (low=O to 2; medium=3 to 5; or high=6 to 9 leaf layers), PLANTS (number of woody plants within 20 cm around the experimental seedlings), UNDER PALMS (whether or not seedlings were located under the crown of and adult palm), FUNGI (seedlings leaf surfaces with or without fungus), HERBIVORY(seedling leaf damage).

Astrocaryum (N=l 15)

Variable	Parameter Estimate	Standard Error	Wald χ^2	Standardized Estimate	p-value χ^2
Intercept	2.1245	0.9871	4.6323	...	0.0314
Microrelief	-0.2723	0.8898	0.0937	0.0522	ns
Leaf Litter	-0.7250	0.4532	2.5593	0.2819	ns
Plants	-0.8228	0.5835	1.9886	0.2000	ns
Underpalms	1.1143	0.6899	2.6085	0.3065	ns
Fungi	0.4327	0.2778	2.4259	0.2682	ns
Herbivory	0.4395	0.6502	0.4570	0.1111	ns

Dipteryx (N=93)

Variable	Parameter Estimate	Standard Error	Wald χ^2	Standardized Estimate	p-value χ^2
Intercept	1.7204	0.8788	3.8326	...	0.0503
Microrelief	-0.8392	0.6499	1.6672	-0.1911	ns
LeafLitter	-0.4741	0.5292	0.8027	-0.1307	ns
Plants	-0.2509	0.1141	4.8341	-0.2873	*
Underpalms	-0.9184	0.5315	2.9857	-0.2545	ns
Fungi	0.2716	0.4943	0.3020	0.0729	ns
Herbivory	0.3572	0.5447	0.4301	0.0878	ns

* $p< 0.05$; ns= not significant, $p>0.10$

Table 7. Pearson Correlation Matrix of factors measured in four $1m^2$ plots located in the comers of each of twenty tive 10 x 10 m subplots. Factors are Mean Leaf Litter Layer (MLL), Mean *Heliconia* Density (HDn, Mean *Tectaria* Density (TDn, Mean Light lncident (MLI), and *Astrocaryum* natural Seedling Density (ASD). See methods for details.

	MLL	HDI	TDI	MLI	ASD
Astrocaryum					
MLL	.				
HDI	-0.224 **(0.305)**	.			
TDI	0.153 **(0.487)**	-0.084 **(0.704)**	.		
MLI	-0.182 **(0.405)**	-0.007 **(0.974)**	0.346 **(0.105)**	.	
ASD	0.118 **(0.591)**	-0.256 **(0.238)**	0.311 **(0.149)**	0.397 **(0.061)**	.

Numbers within parenthesis are p-values for the corresponding correlation coefficients; Bartlet Chi-square statistics=ll.188, DF=lO p=0:343

Table 8. Results of multiple regression analysis of *Astrocaryum* seedling mortality, in plots of 10 x 10 m on Mean LeafLitter Layer (MLL), Mean *Heliconia* Pensity, mean *Tectaria* density ('IDI), *Astrocaryum* Natural Density of Seedlings (ASD) and Mean Light Incident (MLI). See methods for more detail.

	overall regression		$r^2 = 0.545$	n=23	
	SS	MS	DF	F	p
Regression	0.7Sl	0.156	5	4.077	0.013
Residual	1.651	0.038	17		

Partia! regressions (contributions from indepertdent variables)

	Coeff.	t-value	p
Constant	0.198	0.599	0.557
Mean leaf litter layer	0.005	0.065	ns
Mean *Heliconia* density	-0.121	-2.219	**
Mean *Tectaria* density	-0.035	-1.216	ns
Mean Light incident	1.180	3.965	***
Astrocaryum seedling density	-0.024	-2.086	**

*** = p< 0.001; **= p<0.05; ns= not significant

Figure 1. Design of the field experiment to investigate factors affecting *Astrocaryum* and *Dipteryx* post- dispersa! seed survival. Toe squares represent 10 x 10 m plots which were located 20 m apart from each other. Given in each comer are the number of seeds that were set out in lm^2 subplots. Biotic and abiotic factors were recorded within each lm^2 subplot See methods for further details.

AS1ROCARYUM	16 4 32 8	Ll	16 32 8 4	16 8 32 4	8 4 16 32
DIPTERYX	Li	32 8 4 16	4 16 32 8	16 8 32 4	Li
AS1ROCARYUM	Ll	Li	16 8 32 4	8 16 4 32	rl31
DIPTERYX	32 16 4 8	LI	LI	LI	Ll
AS1ROCARYUM	32 8 16 4	Ll	4 16 32 8	4 32 16 8	4 8 32 16
AS1ROCARYUM	Ll	Ll	LI	8 32 4 16	8 4 16 32

Figure 2. Survival of *Astrocaryum andDipteryx* seeds over 20 weeks, June to November of 1992. Values shown represent means ± one standard error (vertical barrs) of the proportions of seeds surviving in the replicates (twenty for *Astrocaryum* and ten for *Dipteryx* of each one of four experimental seed numbers (4, 8 and 16 and 32 seeds).

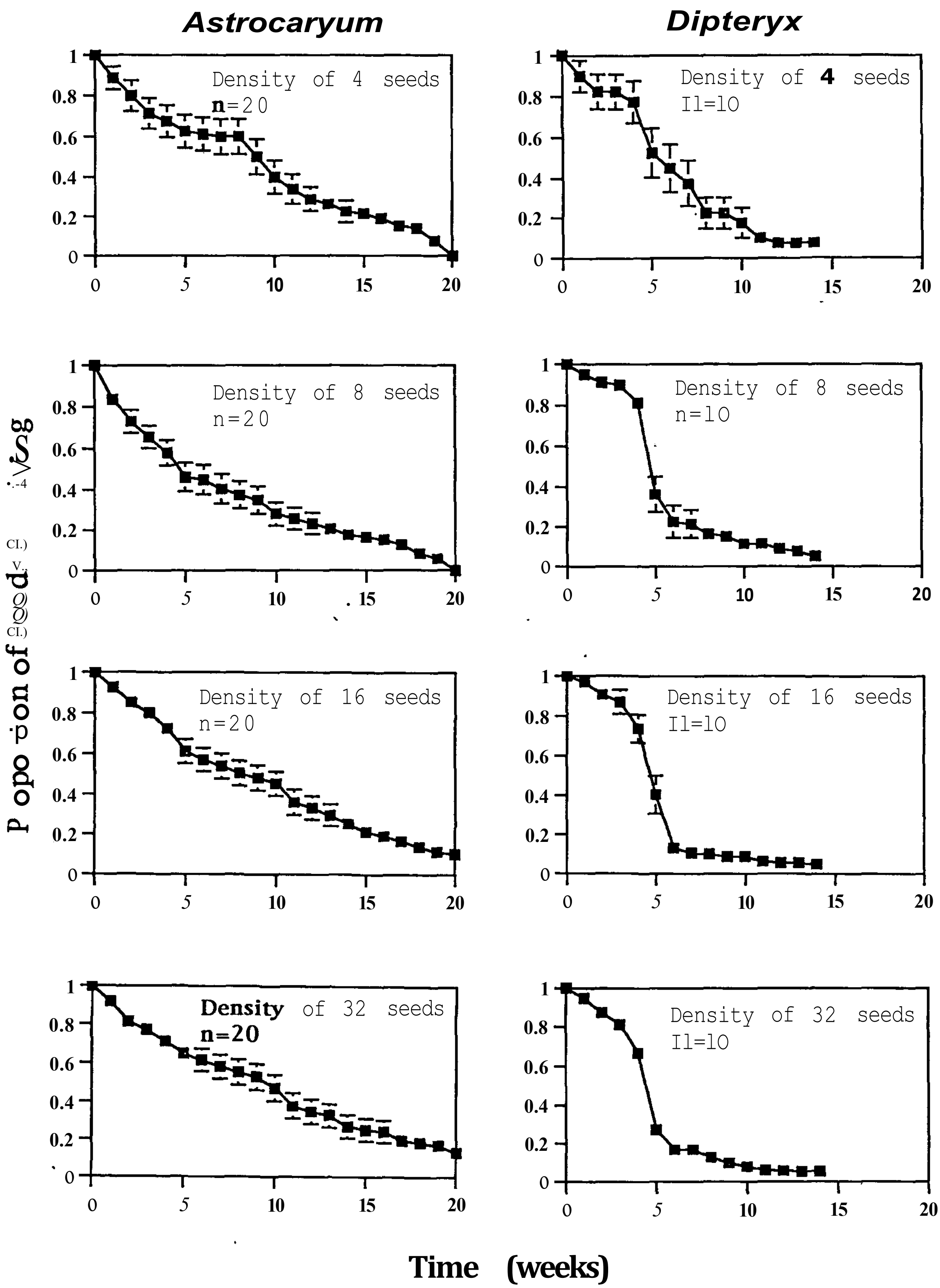

Astrocaryum
Dipteryx
Density of 4 seeds
n=20
Density of 4 seeds
n=10
Density of 8 seeds
n=20
Density of 8 seeds
n=10
Density of 16 seeds
n=20
Density of 16 seeds
n=10
Density of 32 seeds
n=20
Density of 32 seeds
n=10
Time (weeks)

Figure 3. Survival of (a) ***Astrocaryum*** and (b) ***Dipteryx*** seeds under four density treatments (4, 8 , 16, and 32). Toe survival function represents the proportion of the initial population of seeds that was still ative at the start of each weekly census. Significant differences were obtained with all seed densities when early seed survival was emphasized (Wilcoxon's test, x2=20.3, DF=3, p<0.0001) al1 seed densities differed. Similar results were obtained when later survival was weighted more heavily (Log-rank test, x2=22.6, DF=3, p<0.00004).

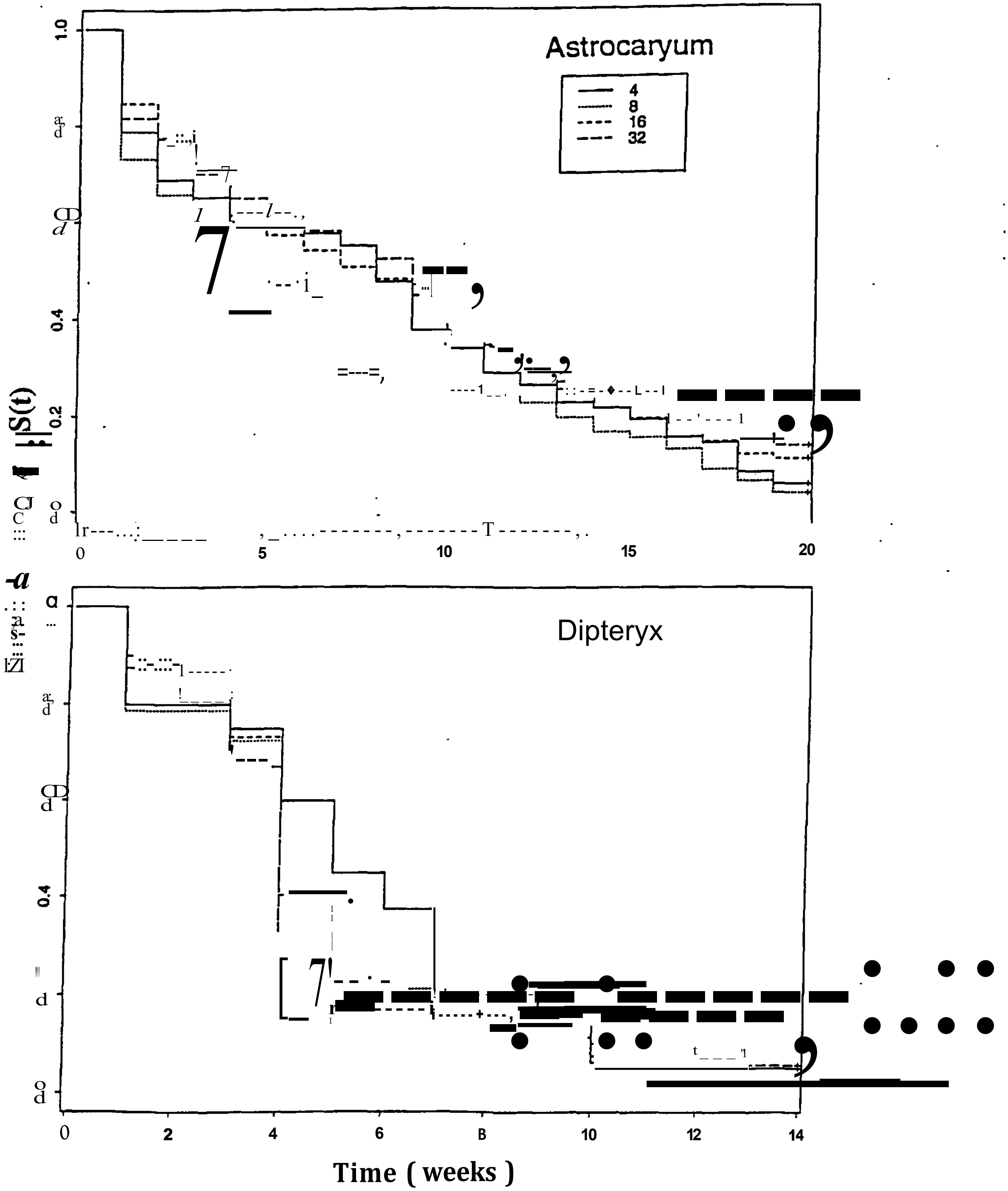
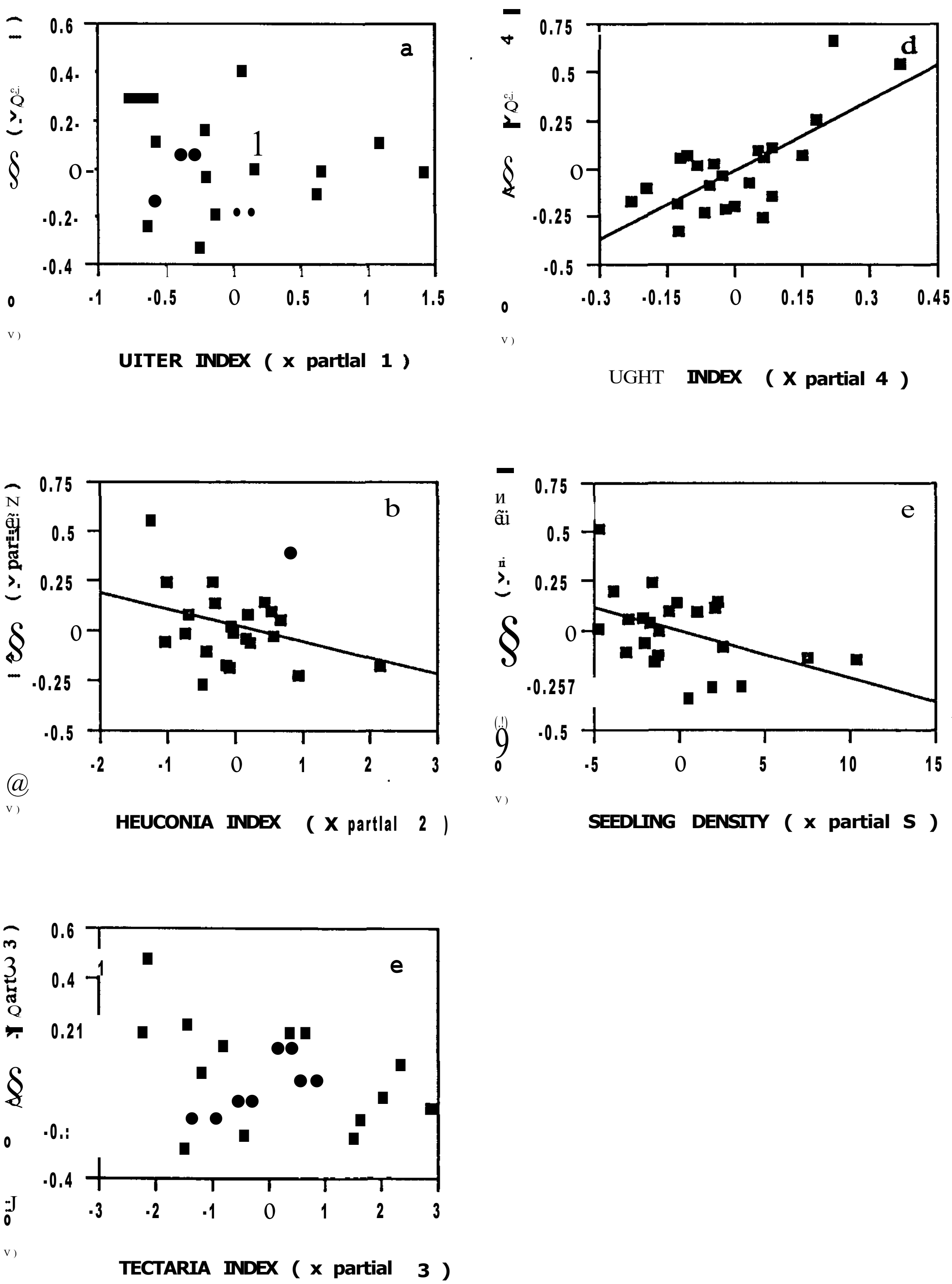

Astrocaryum
4
8
16
32
S(t)
1.0
0.4
0.2
0
5
10
15
20
Dipteryx
0.4
0
2
4
6
8
10
12
14
Time (weeks)

Figure 4. ***Astrocaryum*** seedling mortality as a function of (a) Mean Litter Layer, (b) Mean ***Heliconia*** Density (plants/m^2), (e) Mean ***Tectaria*** Density (plants/m^2), (d) Mean Light Incidence, and (e) ***Astrocaryum*** seedling Density (seedlings/10 x 10 m) (partial ·regressions). See methods for further details.


a
LITTER INDEX (x partial 1)
d
LIGHT INDEX (X partial 4)
b
HELICONIA INDEX (X partial 2)
e
SEEDLING DENSITY (x partial 5)
e
TECTARIA INDEX (x partial 3)

Chapter 2

EFFECTS OF LEAF LITTER COVER AND DEPTH ON EARLY RECRUITMENT OF *Astrocaryum murumuru* and *Dipteryx micrantha*, TWO COMMON AMAZONIAN TREE SPECIES .

Summary

Toe annual amount of leaf litter fall produced by different tree species in tropical forests varies in space and time. Falling litter may cover seeds and thereby enhance their survival by making their detection by seed predators more difficult.

In this chapter I test whether *Astrocaryum murumuru_andDipteryx micrantha* seeds survive better in microsites covered by leaf litter. I experimentally simulated natural conditions by using different seed numbers and modifying the litter cover on the forest floor. I also examined how natural variation in leaf litter cover and thickness affects seed and seedling survival of these two plant species.

Seed survivorship was significantly higher for both plant species at microsites with leaf litter than those with bare soil. Results from an experiment in which the litter was not disturbed showed that *Astrocaryum* seed survival was higher in areas with proportionally higher litter depth. Litter thickness (defined as number of overlying dead leaves present in the sarne site) was positively related to seed survival in this experiment. *Astrocaryum* seedling survival was significatively affected by leaf litter with more seedlings surviving in shallow litter, Whereas leaf litter had no effect on *Dipteryx*

seedling survival. Toe results of the study suggest that the early recruitment of *Astrocarywn* and *Dipteryx* are influenced by the spatial distribution of the amount of forest leaf litter.

Introduction

Toe presence of both deciduous and evergreen trees in many tropical forests may result in significant spatial heterogeneity on the forest floor due to temporal and spatial variation in litterfall (Frankie et.al.1974, Luizão and Schubart 1987, Wright and Comejo1990).

Deep litter may enhance seed survival by creating good conditions (such as less variation on moisture and soil temperature) for germination of large seeds (Sork 1983), and may also hinde seeds from predators. Spatial variation in the amount of leaf litier covering the forest floor may therefore be an important factor which, at various scales, can influence seed survival and seedling establishment (Molofsky and Augspurger 1992). Local variation in leaf litter may also increase the number of regeneration microsites available for plant establishment (Grubb 1977, Bazzaz 1984, Denslow 1980) and it has been given as a partial explanation for high tree species diversity in tropical forests (Ricklefs 1977, Molovsky and Augspurger 1992).

Most empirical studies on the effects of litter on plant populations and communities were conducted in temperate regions (see review in Facelli and Pickett 1991). In the tropics, litter effects have been poorly investigated(but see Schupp 1989, Molovsky and Augspurger 1992). In temperate regions, the presence of leaf litter has been shown to reduce seedling emergence (Reader 1993) and enhance growth of the understory vegetation (Ellenberg 1988). In addition, leaf litter can produce changes effects in the structure of successional communities by shifting dominant species during succession. After removing the leaf litter produced by the dominant plant species ***Setaria faberii,*** Facelli and Facelli (1993) found that the biomass of ***Erigerun annuus*** increased, making this plant species dominant over ***Setaria.***

Spatial variation in leaf litter cover and depth has been suggested as an important factor in community diversity in tropical forests due to its unpredictable stochocasticity (Molofsky and Augspurger 1992). Microsite qualities, such as light, temperature, moisture and nutrient availability, can be modified by the amount of overlying litter with significant consequences for germination and seedling performance (Facelli and Pickett 1991).

Toe role of leaf litter in protecting seeds and seedlings from detection by predators is less well studied. Mammalian seed predators might select foraging areas in accordance with the substrate (i.e presence and amount of litter cover). Rodents mainly locate their food by olfaction (Price and Jenkins 1986). Thick litter could hindes detection of seeds by olfaction. Therefore, the survival probability of an individual seed could depend on small scale events, such as being covered by a fallen leaf, or falling into a crevice. Such as protective role of leaf litter is likely to be more important for small seeds than large ones (Harper 1977). Larger seeds are more likely to be buried by scatterhoarding rodents such as agoutis and spiny rats which have the habit of burying and caching seeds under the leaf litter (Smythe 1989, Forget 1991).

ln this chapter, I compare the survival of ***Astrocaryum*** and ***Dipteryx*** seeds when exposed on the surface versus concealed under leaf litter, and in the presence and absence of understory herbs ***(Heliconia*** spp.). I also investigated the survival of experimental seeds (placed on top of the litter), and naturally occurring seedlings, under natural variations in the amount of leaf litter. To test the hypothesis that microsites covered by leaf litter will favor ***Astrocaryum*** and ***Dipteryx*** seed survival by protecting them from predators, I experimentally simulated natural conditions in my study area by using different seed number and by modifying the litter cover on the forest floor. To investigate how differences in leaf litter cover (proportion of the area of each one of the twenty 1m² plots covered by litter) and thickness (amount of overlaying litter, see methods for details) affect *Astrocaryum* and *Dipteryx* seed and seedling survival, I recorded natural variation in the leaf litter at microsites with experimental seeds with their survival, and at the microsites around (20 cm radius) of naturally occurring seedlings of both plant species.

STUDY AREA - I conducted this study at the Cocha Cashu Biological Station, Manu National Park, Peru. Local annual rainfall is about 2100 mm, and the mean annual temperature is 24 oC. An annual dry season extends from May or June to September or October. A silty alluvial soil produced by periodic flooding of the Manu river underlies the floodplain forest within which the research was conducted. Toe habitat is classified as a mature flood plain tropical forest (Terborgh 1983). Toe forest contains many emergent trees and possesses a complex vertical structure (ferborgh and Petren 1991). lnformation on local plant and animal communities is available in Gentry (1991).

SPECIES INVESTIGAIBD- *Astrocaryum murumuru* is a monoecious palm and one of the the most abundant trees in the area (30 adults/ha). Reproductive individuais vary from 7-20 m in height. Toe flowers mature in December -January and fruit prodution follows in March and April. Brown capuchins *(Cebus apel/a*) and squirrels *(Sciurus* spp.) are the primary seed dispersers. After they have fallen to the ground, seeds are scatterhoarded by secondary dispersers, including squirrels *(Sciurus* spp.), agoutis *(Dasyprocta variegata)* and other rodents. Toe sarne animais prey upon the seeds which are also consume<}. by peccaries *(Tayassu pecari* and *T. tajacu)* and insects (Bruchidae). Some trees may produce up to three racemes in a given season and these may ripen up to 900 fruits. Toe nuts (seed plus endocarp) are 2.7-4.8 cm in length by 2.2-2.8 x 1.6-2.4 cm in width (n=lO), and weigh 7.4 ± 1.08 grams (5.4-8.9; n=ll). ***Astrocaryum*** seedlings typically display only 1-2 bifid leaves which are light green above with a characteristic white undersurface. Seedling height (cm) is, 18.6 ± 0.6l(N=42). Natural seedling density varied from 1 to 5/m^2 within one meter radius around adult tree trunks. Leaf damage by insects (crickets) and seedling predation by mammalian herbivores (deers, agoutis,tapirs) are also common.

Dipteryx micrantha is a caesalpinoide leguminous tree that attains heights up to 60 m (mean=44 m, N=32). Typically the trunks are salmon-colored and strongly buttressed. The buttresses of a large individual can extend up to 4-5 m. At Cocha Cashu, the density of adult ***Dipteryx*** trees (2-6/ha) is much lower than that of Astrocaryum palms. ***Dipteryx*** flowers in November at the beginning of the wet season, producing large showy panicles of purple flowers. The single-seeded drupes ripen by June or July. Ripe fruits are primarily dispersed by bats, which chew off the fleshy exocarp and drop the endocarp containing the intact seed under their feeding roosts. Mammals such as spiny rats, agoutis, and squirrels disperse and also eat the seeds. Consumption and dispersa! of ***Dipteryx*** seeds is concentrated in the dry season when few other tree species are fruiting. An adult ***Dipteryx*** tree may produce up to 1000-1500 fruits. Toe drupe is indehiscent. Fruit dimensions (including seeds)are, length: 3.0-6.0 cm, width: 1.8-3.8 x 1.5-3.0 cm width. Fruits weigh 21.5 ± 2.92 grams (8-40; n=l 1). Seedlings present two fleshy cotyledons (which last about two weeks), and two compound leaves, each with 6-10 leaflets. At the completion of germination seedlings are about 30 cm high (mean 28.96 ± *0.55;* range 17.5-40; n=54). I recorded seedling densities between O.O1 to 0.56/m^2 under parent trees.

Methods

In November 1991, I marked seedlings ofboth plant species with numbered aluminium tags within a series of 100 m transects (10 m width)in order to follow their survival. Seeds of both plant species were collected in May 1992 under fruiting trees and at bat roosts located at least 1 km from the experimental sites. All experimental seeds were checked to see whether they were intact, and only those fresh and in good condition were used. Each individual seed was marked with a sharp-point permanent marker.

To quantify spatial variation in leaf litter thickness at the sites where the experiments were conducted, I inserted my Swiss army knife in the leaf litter at 1 m intervals along two 150 m parallel transects (the same used for the experiments 1 and 2, see experimental designs), and counted the number of dead leaves it pierced. Experimental plots 1 ^{2} in area were prepared one week before the beginning of the experiments and left without seeds. I used a small mattock to clear and remove the litter, which was then removed to another area 30 m away from the plots. Seed survival experiments were initiated in June *(Astrocaryum*) and July *(Dipteryx)* of 1992. The positions of the seeds in each $1m^2$ experimental plot within the 10 x 10 m blocks, were marked with colored tooth picks.

THE EFFECTS OF LEAF LITIER ON SEED SURVIVAL

DESIGN OF EXPERIMENTS:

EXPERIMENT 1- THE EFFECTS OF LEAF LITTER ON *Astrocaryum* and *Dipteryx* SEED SURVIVORSIDP

To investi.gate the effects of the presence of leaf litter cover on ***Astrocaryum*** and ***Dipteryx*** seed survival, I used a factorial design with the following four treatments: 1) seed densiti.es above the leaf litter; 2) seed densiti.es under the leaf litter; 3) seed densiti.es over bare soil (subplots with total remova! of leaf litter); 4) seed densities protected by a metallic cage (made with chicken wire mesh). The four treatments were assigned randomly to ten 10 x 10 m plots separated by 5 m from each other, along a 150 m transect Using a metric tape I subdivided each of the ten 10 x 10 m plots in 100 subplots of $1m^2$ which were all numbered from 1 to 100. Then using a random number table, I selected the positions of twelve $1m^2$ subplots within each of the 10 x 10 m plots (Figures 1 and 2). The replicate sets of ***Astrocaryum*** and ***Dipteryx*** experimental seeds (4, 8 and 16 seeds/ m^2) were arrayed evenly within each one of the twelve $1m^2$ subplots, with the four treatments, making four replicates of each seed density treatment, one seed density replicate for each of the three litter treatments and one for the metalic cage treatment within each 10 xlO m plots (Figure 1). ln the fourth treatment, I placed 4, 8 and 16 intact seeds within 30 x 30 cm wire mesh bags. The bags were made with 1 cm^2 mesh, and prevented vertebrate attack while permitting bruchids to pass through.
I distributed 30 bags arnong the sarne ten 10 x 10 m plots, using the sarne protocol as for the other three treatments.

The experiment was checked weekly over seven weeks for seed attacks by mammals and bruchids. Fallen dead leaves were removed weekly from the bare soil treatments weekly in order to maintain exposure of the seeds in those treatments.

STATISTICAL ANALYSIS- I compareci seed survival curves among the blocks, seed number and litter treaments. The analysis employed Cox models fitted to the survival curves using the Cox Proportional Hazard Regression procedure available in Splus (1991). This procedure entails a binomial log-log regression that combines all censuses into a single test, correctly using right-censored data (i.e. those seeds still surviving at ttie end of the experiment for which the total survival times were not known). Toe Cox procedure calculates the parameter "survival function," a survivorship curve, which represents the proportion of the initial seed population still present at each census. (for examples of ecological studies using this analysis see Schupp 1990 and Pyke and Thompson 1986).

To test for equality of survival curves, and to compare survival functions among experimental blocks, seed number, and litter treatments, I used both the Mantel-Haenzel test (Log-Rank test), and Peto-Peto's test (a modification of the Gehan-Wilcoxon test), both available in Splus (1991). I employed the two tests because they emphasize different portions of the survival curves. Toe former emphasizes late survival, while the latter test emphasizes early survival (Splus 1991).

For experiment 1, I also used a :t'ully crossed factorial analysis of variance (ANOVA), available in GLM-procedure (SAS 1987). In this analysis, *Astrocaryum* and *Dipteryx* seed survival (using the response variable, " time to 50% seed survival" were analyzed separately in relation to the categorical variables such as blocks, treatments (seeds in bare soil, below and above leaf litter) and seed number. Blocks, treatments and seed number were treated as fixed effects. I used time to 50% seed survival because it provides a sensitive criterion for comparison.

Because l used different seed numbers, l verified the existence of bias in the estimates of the least-squares estimates, using the weight statement available in MGL-SAS and ran the sarne factorial analysis of variance. Toe values and signiticance leveis found were similar to those for the factorial ANOVA with non weighted least-squares, indicating that the weights of the observations were proportional to the reciprocais of the error variances, and that the weighted least-squares estimates gave the best linear unbiased estimators.

To verify which means of the response variables were different from one another· under different leaf litter treatments, l used a post-hoc test (Duncan multiple range test) also available in the MGL procedure of SAS. Duncan's test uses a studentized range statistic. This test controls the type l error rate at alpha=0.05.

EXPERIMENT 2- EFFECTS OF VARIATION OF SPATIAL SCALE WITH LEAF LITI'ER COVER AND ASTROCARYUM SEED SURVIVAL

Toe second experiment of this chapter was designed to assess the effect of leaf litter on ***Astrocaryum*** seed survival at different (smaller) spatial scales. Here l used eight seeds eve y arrayed per $1m^2$ subplot, instead of three different seed numbers, each placed in a $1m^2$ subplot (Figure 1). Toe $1m^2$ subplots were chosen randomly using the sarne method as in experiment 1. ln each $1m^2$ subplot, the natural litter was modified according to the following four treatments: 1) zero percent litter cover (litter removed from the whole $1m^2$ subplot); 2) twenty tive percent of the $lrri^2$ plot with litter cover; 3) tifty percent of the $1m^2$ plot with litter cover; 4) seventy tive percent of the $1m^2$ plot with litter cover. ln all treatments litter cover was applied to a depth of approximately 3 cm. Litter cover treatments were randomly assigned and replicated four times for each treatment, making a total of sixteen 1 m^2 subplots within each of the ten 10 x 10 m plots. Toe 10 x 10 m plots were separated by 5 m one from another, in the sarne disposition as in the first experiment, and alonga 150 m transect (see Figure 1).

STATISTICAL ANALYSIS- 1 used the MGLH procedure in Systat (Wilkinson 1991). 1 ran an analysis of variance (Two-way ANOVA) and analyzed the effects of blocks, the four treatments (bare soil or O% cover, 25%, 50% and 75% covered by leaf litter) and interaction between blocks and treatments with "number of weeks that seeds survived" as response variable. This response variable was used because the sarne seed density (8 seeds) was used in all treatments, which makes the initial condition the sarne. A. Duncan multiple range test was also used as in the first experiment to verify differences arnong means of the response variable (number of weeks seeds survived) under different treatments.

EXPERIMENT 3- SPATIAL VARIATION IN THE AMOUNT OF NATURALLY OCCURRING LEAF LITIER AND *Astrocaryum* SEED SURVIVAL

In a third experiment, I investigated whether natural variations in the spatial distribution of litter cover, litter depth· and understory vegetation affect *Astrocaryum* seed survival. This experiment serves as the control for the other two because here leaf litter was not disturbed in creating experimental treatments. I set up this experiment in the first week of July 1992. Because I did not have enough *Dipteryx* seeds, I used only *Astrocaryum* seeds for this experiment.

I used eight parallel transects, 100 m long and 20 m apart, with five 10 x 10 m plots along each transect, each separated by 20 m. Toe transects were located approximately 200 m from the first two experiments. Four seeds were placed evenly within $1m^2$ subplots located at the center of each 10 x 10 m plot. Altogether there were 20 groups of 4 seeds each. Seeds were checked for survival weekly for 20 weeks.

In order to estimate the litter cover, I held a $1m^2$ PVC frame subdivided into 25 x 25 cm squares 50 cm above each experimental subplot and counted the number of 25 x 25 cm subdivisions covered by leaf litter on the ground. I used the proportion of squares covered by litter as a litter cover index (LCI). I measured litter depth at the four corners of the frame using a metallic centimeter scale by inserting it through the litter until it touched the soil. Toe litter depth index (LDI) for each plot was the mean of these four measurements. I also counted the number of 25 x 25 cm squares covered by *Heliconia* leaves and divided by 25 to generate a *Heliconia* cover index (HCI) for each subplot.

STATISTICAL ANALYSIS- In experiment 3, I used multiple regression analyses (Systat-MGLH, Wilkinson 1991) to investigate effects of factors such as litter depth (LDI), litter cover (LCI) and understory vegetation cover (HCI) on seed survival. Because I used only one seed density in this experiment, the initial conditions for the experimental groups of seeds were the same. Toe maximum number of weeks *Astrocaryum* seeds survived was used as the response variable.

THE EFFECTS OF LEAF LITTER ON SEEDLING SURVIVAL

First, in a preliminary experiment I covered 10 germinating seeds (which were collected in the forest floor and kept inside a 2 x 1 m enclosure) of *Astrocayum* and *Dipteryx* to a depth of 10 cm with leaf litter, and protected the seeds in a hard wire mesh cage. After two months, all twenty seedlings emerged alive from the litter. Two *Dipteryx* seedlings had been attacked by fungus but were still alive. Apparently the litter does not act as a physical barrier to seedling emergence. Then I asked whether microsites covered by large amoun,ts of leaf litter would offer seedlings more protection (from predators) than microsites with less litter. Using a random number table, I selected 115 *Astrocaryum* seedlings and 197 *Dipteryx* naturally occurring seedlings from a much larger population of seedlings of both species, which in October 1991, were mapped and tagged in a 2.5 ha plot in the sarne study area. At the location of each plant, I recorded the number of leaf litter layers and whether or not the seedling was shaded by an overtopping *Heliconia* plant. Leaf litter depth was assigned categorical values as follows: 1-low (1-2 layers); 2-medium (3-5 layers); 3-high (6-9 layers).

I censused the seedlings for survival five times between October 1991 and October 1992. I was able to distinguish mortality produced by predation from that caused by other factors. A few seedlings were damaged by fallen branches, and none of them died. Mortality of *Dipteryx* seedlings was ascribed to mammal predation when the stems were nipped off (with both compound leaves also being removed) or when cut at the stem base (about 5 cm height). Sometimes, mammals browsed the whole *Astrocaryum* seedling, by cutting it at the stem base, or by pulling up the whole plant and consuming. the seeds as well.

STATISTICAL ANALYSIS- I used logistic regression analysis available in the Logistic procedure (SAS 1988) to analyze the effects ofleaf litter layers (or number oflayers of leaves countend at 10 cm radius of each seedling) on the survival of *Astrocaryum* and *Dipteryx* seedlings.

Results

SPATIAL VARIATION OF LEAF LITIER lN Tiffi FOREST

Toe following results describe the spatial variation in leaf litter thickness at the sites where the experiments 1 and 2 were conducted. ln experiment 1, the natural variation in the number of leaf litter layers along the 150 m transect (ten 10 x 10 m plots) ranged from 1 to 8 layers. Plot 9 was the most variable, yielding a range of 3-8 leaf layers (Figure 2). There was significant variation between plots in the number of leaf litter layers (On.e-way ANOVA, F= 2.77; DF=9; p=0.006). ln the 150 m transect (ten 10 x 10 m plots) where the experiment 2 was conducted, the number of leaf litter layers also varied between one and eight leaf layers. Plot 1 was the most variable (Figure 2). However, in this transect, there was no significant between-plot variation in the number ofleaf litter layers (One-way ANOVA, F=l.64; DF=9; p=0.114).

EFFECTS OF LEAF LITIER ON *Astrocaryum* SEED SURVNAL

ln this paragraph I present the results óf experiment 1 in which I investigated the effects of leaf litter on *Astrocaryum* seed survival. By comparing whole survival curves (using Cox Hazard Regressions models), and by analyzing time to 50% survival (using Factorial Anova), I found significant differences in s survival among the three litter treatments (fables 1, 2 and 4). Survival of *Astrocaryum* seeds was poor on bare soil relative to under and above the litter (fable 4 and Figure 4).There were no significant block effects, indicating no spatial differences among the experimental blocks (ten 10 x

10 m plots) on *Astrocaryum* seed survival (Table 2), and no significant interactions between blocks and litter treatments (Table 2). There were no significant effects of seed number (Table 2) on seed survival initially, and no significant effects over the whole period of the experiment (Table 1 and Figure 4 and 6). Therefore, the survival probability of *Astrocaryum* seeds in the presence of leaf litter appears not to be dependent on the number of seeds present. Although *Astrocaryum* seeds protected by hard wire mesh bags were not attacked by mammals, insect predation on the protected seeds was clearly dependent on number of seeds ($r=0.92$, $DF=1$, $F=158.9$, $p=0.000$).

EFFECTS OF LEAF LITTER ON *Dipteryx* SEED SURVIVAL

In the case of *Dipteryx*, there were a significant differences in *Dipteryx* seed survivorship under the three litter treatments (Tables 1, 2 and 4, and Figures 5 and 6). As with *Astrocaryum* seeds, mammalian seed predators attacked exposed seeds on bare soil faster than those on or under litter cover. This was true both initially and over the whole period of the experiment (Figure 4). Initially, there were no significant block effects on seed survival (time to 50% survival) indicating no spatial variation in seed survival among the experimental 10 x 10 m plots. Seed number did not affect *Dipteryx* seed survival (Table 2). However, block effects on seed survival were detected when the entire survival curves were compared (Table 1).

LEAF LITTER AND SEED GERMINATION- A higher percentage of seeds germinated under the litter than on the bare soil or on top of the litter. Forty-eight of 53 *Dipteryx* seeds (90.5%) germinated under the litter. Eleven of 13 surviving seeds (84.6%) germinated on top of the litter, and only nine of 20 surviving seeds (45%) germinated on bare soil.

Only five ***Astrocaryum*** seeds were observed germinating in this experiment (experiment 1) (four under and one above the litter) and none of them produced a surviving seedlling. I did not observe any ***Astrocaryum*** seedling produced by the experimental seeds. Only nineteen ***Dipteryx*** seedlings were produced. At the end of the experiment, fifteen ***Dipteryx*** seedlings were still ative.

SEED SURVIVAL AND SPATIAL VARIATION 1N LEAF LTITER AT SMALLER SCALE

ln order to investigate how leaf litter affects ***Astrocaryum*** seed survival at smaller spatial scales than that used in experiment 1, I reduced the area covered by litter in $1m^2$ subplots within ten 10 x 10 m plots located in another transect 150 m long. I used clifferent percentages of the area of the $1m^2$ experimental subplots with litter covering the seeds (treatments were: O, 25, ***50*** and 75% of litter cover). Toe number of seeds used (8 seeds) was the sarne per treatment. There were significant differences in the maximum time of ***Astrocaryum*** seed survival (number of weeks) among treatments (Table 3 and 4). Seed survivorship was significantly higher in subplots with 50% of litter cover than in subplots with bare soil (Figure 7). No significant clifferences in seed survival were found between subplots with 25% and 75% of litter cover. Again survival of ***Astrocaryum*** seeds was poor on bare soil subplots relative to those plots with ***50*** % of their surface covering the seeds. Also there were significant block effects indicating spatial variation in seed survival. However, there were no-interactions between block and litter treatment effects on ***Astrocaryum*** seed survival (Table 3).

Astrocaryum seed survival was analyzed with respect to the depth and cover of naturally occurring leaf litter in experiment 3 (Table 5). Only litter depth and litter cover significantly affected the survival of ***Astrocaryum*** seeds (Table 6, and Figure 6), confinning earlier results from experiment 1. Understory vegetation cover had no effects on *Astrocaryum* seed survival after 20 weeks (fable 6 and Figure 7).

THE EFFECTS OF LEAF LITIER AND UNDERSTORY VEGETATION ON SEEDLING SURVIVAL

The survival of *Astrocaryum* and *Dipteryx* seedlings followed different pattems. Leaf litter thickness significantly affected the survival of *Astrocaryum* seedlings but not that of *Dipteryx* seedlings (fable 7). Microsites with shallow litter offered significantly less protection to *Astrocaryum* seedlings than those with dense litter. Although many *Dipteryx* seedlings were pruned at the meristem by herbivores, they sprouted a new leaf after two months, suggesting that this species can recuperate after partia! predation.

Discu ion and conclusions

Toe results of this chapter indicate that the survival chances of large seeds, such as those of *Astrocaryum* and *Dipteryx*, are higher in microsites covered by leaf litter than in areas not covered by leaf litter (Tables 1 to 5). Even small differences in the area covered by leaf litter (experiment 2) were enough to enhance seed survival. Toe number of weeks *Astrocaryum* seeds survived in 1 m^2 subplots was significantly higher in microsites with 25%, 50% and 75% litter cover than without litter. This result indicates that seed survivorship may be dependent on the presence of leaf litter at a small spatial scales. Just one dead leaf covering a seed could reduce its chances of being located by a predator (Harper 1977).

I found a significant and inverse relationship between litter cover and number of weeks *Astrocaryum* seeds survived (Experiment 3). I also found a significant positive relationship between litter thickness and seed survivorship (Table 6 and Figure 7). Toe abundant and large-leafed understory *Heliconia* plants had no apparent effects on seed survival in either *Astrocaryum* or *Dipteryx* . Threfore areas in the forest with thicker litter will be safer for large seeds and seedlings than areas with shallow litter.
This indicates that spatial variation in the presence and amount of litter is important, because it generates spatial heterogeneity, and consequently may amplify the spectrum of plant regeneration niches (Grubb 1977).

Variation in leaf litter parameters had different effects on seedlings of the two plant species. *Dipteryx* seedling survival was not significantly affected by the leaf litter thickness (here measured as number of overlying leaves). However, leaf litter thickness had significant effects on *Astrocaryum* seedling survival. Toe negative relationship between leaf litter cover and *Astrocaryum* seedling survival suggests that seedlings of this species do better in sites with shallow than in sites with thick litter (Table 7).

Another finding of the experiments is that *Astrocaryum* seed survival under litter protection was independent of seed number. Seeds in groups of 4, 8 and 16 experienced increased survival in microsites with leaf litter relative to those with bare soil, independent of the group size. These results were valid both initially (Table 2) and over the entire experiment period (Table 1).

It can be concluded that the presence and variation in the amount of leaf litter will have different effects on different plant species in the forest Furthermore, the magnitude of the effects will depend on the pattem of distri.bution and abundance of leaf litter within the forest (Molovsky and Augspurger 1992 and this study). Plant species with small seeds, as well as those with big seeds that germinate quickly, may be more likely to escape from predators. Large seeds, such as those of *Astrocaryum* and *Dipteryx* , are more easily found by an animal scanning at ground level. *Astrocaryum* and *Dipteryx* seeds lie on the forest floor at the time (dry season) when the highest input of leaf biomass is falling from canopy (Luizão and Schubart 1987) and thus may benefit from the accumulating litter.

LEAF LIITER AND BEHAVIOR OF SEED PREDATORS

Two important seed predators at Cocha Cashu, the agouti and spiny rat remove the litter in searching for food and, by chance, may uncover large seeds. Agoutis also cover seeds with leaves (pers. obs.), perhaps preventing other competing seed eaters from finding them. Arboreal squirrels and rats such as the spiny tree rat *(Mesomys hispidus)* also forage on the forest floor. Although rodents sometimes scatterhoard and disperse seeds, they are mainly seed predators (Price and Jenkins 1986).

In the Guianan rain forest, Forget (1991) found that the spiny rat, in adition to being a major predator on *Astrocar.yum* seeds, hides *Astrocaryum* seeds under the leaf litter. At Cocha Cashu I found only five *Astrocaryum* seeds buried under the litter. These were seeds from another experiment which had been marked with 20 cm lengths of fishing line. This suggests that rodent species may have generally similar behavior in relation to large seeds such as those of *Astrocaryum* . Therefore, I would expect that rodents would select areas covered by thick leaf litter t(? store seeds.

In other forests, the protection by litter has been found not to be important to seed survival. Among various plant species in an Australian rain forest, only one, in just one part of a replicated experiment , showed higher seed survival in the thick litter treatment (Wilson 1988). In a Panamanian rain forest, Schupp (1989) found seed survival in the very abundant treelet, *Faramea occidentalis* , to be independent of the amount of litter on the forest floor. However, his result may have been influenced by the rodent abundance at BCI, which is much higher than at Cocha Cashu (Glanz 1991).

Toe mechanic protection afforded to seeds by leaf litter may be relative and short-lived. Because few plant species fruit during the dry season, vertebrate seed eaters must rely on a few keystone species, such as *Astrocaryum* and *Dipteryx* , to meet their metabolic needs (Terborgh 1986). Food scarcity may prompt seed eaters to invest significantly higher amounts of time in searching during the dry season than in the wet season , and seeds may not survive long periods. In fact, few seeds survived until the end of the experiments.

However, the positive overall effects of leaf litter on seed survival would be important if the greatest leaf fall were to follow the period of seed dispersa!, which is the case of *Astrocaryum* and *Dipteryx* , in which secondary seed dispersa! occurs during the dry season.

LEAF LlTIER AND ABIOTIC FACTORS

Toe mechanical protection of leaf litter cover on seeds could contribute to the creation of good microsite conditions (humidity and temperature) for seed germination. These two abiotic factors could be criticai to the maintainance of seed viability through the sometimes extreme droughts that occur during the dry season (Fisher et. al 1991). However, variations in the amount of litter present at a given microsite can reduce or favor seedling survival, depending on the plant species and light conditions (Molovsky and Augspurger 1992). Leaf litter apparently is more important for *Astrocaryum* than *Dipteryx* seedlings. Significantly greater numbers of *Astrocaryum* seedlings died where there was more leaf litter (Table 8). Such relative effects on early plant recruitment may create opportunity for partitioning regeneration niches as predicted by Grubb (1977).

At the level of the plant community, the litter mat acts as a physical barrier for seeds and seedlings, because it prevents seeds from reaching the soil and seedlings from emerging and sprouting (Facelli and Pickect 1991, Molofsky and Augspurger 1992). Toe mechanical effects of litter can also limit layers of ground vegetation in deciduous forests (Persson et al., 1987). However, leaf litter may have more pronounced effects on species what produce small seedlings, as demonstrated by Molofsky and Augspurger (1992). They found that ali the smaller-seeded species they studied at BCI were negatively affected by litter, although the degree varied with the plant species. For shade intolerant species, such as *Luehea seemannii, Ochroma pyramidale* and *Ceiba pentandra* , they found the presence and amount of litter to have different effects on their seedlings. Toe presence of even smalJ amounts of litter was enough to inhibit *Luehea,* while only thick litter had negative effects on seedling emergence in the other two species.

Litter effects are not always independent of the effects of other factors. Molofsky and Augspurger (1992) found that more *Gustavia* seedlings established under litter in the sun, whereas the presence of litter had no effect on seedlings in the shade. More generally, they found that the effect of litter on seedling e ergence depends on the size of the seedling and plant species considered.

EFFECTS OF LEAF LITIER ON SEED GERMINATION AND SEEDLING EMERGENCE

The available data suggest that the presence of litter is important for the germination of *Dipteryx* seeds, and more important for *Dipteryx* than *Astrocaryum* seeds. The number of seeds germinating under litter was about four times higher than above litter.

The potentialy negative physical effect of litter may not be criticai for the emergence of *Astrocaryum* and *Dipteryx* seedlings, although it does affect *Astrocaryum* seedling survival (fable 7). In both *Astrocaryum* and *Dipteryx,* the radicle and the first sprouting stem are relatively lignified, making them hard to break apart (pers. obs), and thus may be relatively resistant to fallen debris and herbivore attack. These anatomical and structural characteristics are typical of tropical tree species with short periods of seed dormancy, and they may help germinating seeds to perforate the physical barrier created by leaf litter mat.

Dry leaves are lighter and probably more easily perforated or raised by the radicle of an emerging seedling. However, local concentrations of relatively broad, thick dead leaves such as those of *Matisia* spp. may create a heavy litter layer which could result in negative effects on *Astrocaryum* and *Dipteryx* germination and seedling emergence.

Toe leaf litter created by fallen palm leaves produces shade and may also have negative effects on seedling survival. Fallen *Astrocaryum* ! aves around the parent tree could have negative shading effects on seedlings. However, the accumulation of fallen *Astrocaryum* leaves, with their long, strong spines, might also have a positive effect on seed survival by discouraging rodent foraging. But such an effect on seed survival would be relative, because small insect predators, such as bruchids, could pass through the spines without injury and attack the seeds.

LEAF LITTER AND POPULATION RECRUITMENT OF *Astrocaryum* and *Dipteryx*

Toe seeds of both *Astrocaryum* and *Dipteryx* contain reserves that may help them resist the vaguaries of an unpredictable environment e.g.,: 1- being covered by a temporary and thick leaf litter layer; 2- desiccation during the dry season; 3- flooding in the wet season; 4- scatcity of soil micro- and macro-nutrients; 5- shading by other plants. However, the seedling would receive this benefit only during its first year, after establishment After that, seedlings become independent of parental reserves stored in the endosperm *(Astrocaryum)* or cotiledons *(Dipteryx)* and must cope with all biotic and abiotic factors of their microsites.

Finally, leaf litter can produce both positive and negative effects on seeds and seedlings of large-seeded trees. Toe intensity of the effects however will depend on many other factors, including features of the microsites. The phenological behavior of the plant community, for example, determines the quantity and seasonal timing of litterfall.
The spatial relations of adult trees of different species will determine the spatial distribution and thickness of the litter in the forest. However the variation in amount of litter and spatial location of the microsites in which the seedlings are established could be

important for seed and seedling survival as this study suggests. Toe results of this study in general suggest that the early recruitment of *Astrocaryum* (seed and seedling survivorship) and Dipteryx. (seed survivorship) are leaf litter dependent.

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Table 1. Survival of *Astrocaryum* and *Dipteryx* seeds in relation to ten experimental blocks, three seed number treatments (4, 8 and 16), and three leaf litter treatments (seeds on bare soil, above and under leaf litter) (Cox Proportional Hazard Regression).

Parameter	DF	Estimate(SE)	z	Sig. level
Astrocaryum +				
Block	10	0.029 (0.024)	2.31	*
Leaflitter	3	-0.286 (0.045)	-6.38	***
Seednumber	3	0.098 (0.007)	1.31	ns
Dipteryx ++				
Block	10	-0.022 (0.012)	-1.76	*
Leaflitter	3	-0.311 (0.043)	-7.33	***
Seednumber	3	0.014 (0.007)	1.83	ns

***, $p<0.0001$; **, $p<0.001$; *, $p<0.05$; ns, not significant.
+Likelihood ratio test=49.4 on 3 DF, $p<0.000001$;
++ Likelihood ratio test=61.2 on 3 DF, $p<0.000001$.

Table 2. Results of factorial Analysis of Variance (ANOVA) of response variable "time to 50% seed survival," (weeks) on independent variables: a) experimental blocks (first level, with ten blocks for ***Astrocaryum*** and ten blocks for ***Dipteryx***); b) treatments (second level, with three treatments: 1-seeds on bare soil; 2-seeds above litter; 3-seeds under litter); e) seed number (third level, with three seed number, or 4, 8 and 16 seeds/lm^2). See text for further details.

Source of variation	SS	DF	MS	F
Astrocaryum +				
Block	6.379	9	0.709	7.36***
Treatment	2.068	2	1.034	10.74***
Seednumber	0.129	2	0.064	0.67ns
Block*treatment	1.686	18	0.094	0.97ns
Block*seed number	0.871	18	0.048	0.50ns
Treatment*seed number	0.036	4	0.009	0.09ns
Block*treatment*seed number	3.466	36	0.096	
Dipteryx				
Block	10.789	9	1.199	1.21ns
Treatment	23.217	2	11.608	11.70***
Seednumber	3.617	2	1.808	1.82 ns
Block*treatment	16.561	18	0.920	0.93ns
Block*seed number	11.828	18	0.657	0.66ns
Treatment*seed number	6.667	4	1.666	1.68ns
Block*treatment*seed number	35.722	36	0.993	

+ For ***Astrocaryum,*** the response variable, "time to 50% seed survival" was root-square transfonned to approximate a normal distribution. *** p=0.0001; ns=not significant.

Table 3. Results of two-way Analysis of Variance (ANOVA) of response variable "number of weeks *Astrocaryum* seeds SU1Vived," in ten experimental blocks, under four leaf litter cover treatments (seeds on bare soil or 0% litter cover, and 25%, 50%, 75% of leaf litter cover). See methods for additional details.

Source of variation	*SS*	DF	MS	F
Block	32.100	• 9	3.567	3.025*
Litter treatments	28.925	3	9.642	8.177***
Block*litter treatment	29.450	27	1.091	0.925ns
Error	141.500	120	1.179	

***= p<0.000; ** = p<0.01; ns=not significant

Table 4. Results of Duncan multiple comparison test of means for time at seed 50% survival, from the experimental treatments (seeds under and above litter and in bare soil) for ***Astrocaryum*** and ***Dipteryx*** (Experiment 1) and experimental treatments (Seeds in bare soil, 25%, 50% and 75% covered by litter) for ***Astrocaryum*** seeds (Experiment 2). See methods for more details.

Treatments	n	Mean value	Duncan Grouping*	
Experiment 1				
Astrocaryum				
Under litter	30	1.307	b	
Above litter	30	1.054	b	
Bare soil	30	0.946		a
Dipteryx				
Under litter	30	3.883-	**b**	
Above litter	30	3.050	**b**	
Bare soil	30	2.667		a
Experiment 2				
Astrocaryum				
50% cover	40	2.375		a
75% cover	40	2.100	b	
25% cover	40	1.850	b	
Bare soil	40	1.225		e

***equal letters = treatment means are not significantly different; different letters = treatment means are significantly different**

Table 5. Pearson Correlation Matrix for Leaf Litter Cover Index (LCI), Leaf litter Depth Index (LDI), and Vegetation Cover Index (HCI).

	LCI	LDI	HCI
LCI	.		
LDI	0.294 (0.209)	.	
HCI	0.137 (0.564)	-0.088 (0.711)	.

Numbers within parenthesis are p-values for the correlation coefficients; Bartlet Chi-square statistics=2.196, DF=3 p=0.533

Table 6. Results of multiple regression analysis, with response variable ▪ number of weeks *Astrocaryum* seeds survived, on independent variables: Leaf Litter Cover Index LCI (%), Leaf Litter Depth Index LDI (%), and Vegetation Cover Index HCI (%). See methods for more details.

Overall Regression $r^2 = 0.441$ n=20

	SQ	MS	DF	F	p
Regression	327.529	109.176	3	4.213	0.022
Residual	414.671	25.917	16		

Partia! regression (contributions from independent variables)

	Coeff.	t-value	p
Constant	89.845	2.979	0.009
Leaf Litter Cover	-89.543	-2.791	0.013
Leaf Litter Depth	3.708	2.793	0.013
Vegetation Cover	6.462	·1.497	0.154

Table 7. Results of Logistic Regression Analysis of the response variables *"Astrocarywn* and *Dipteryx* one year seedling survival" on leaf litter thickness.

Analysis of maximum likelihood estimates

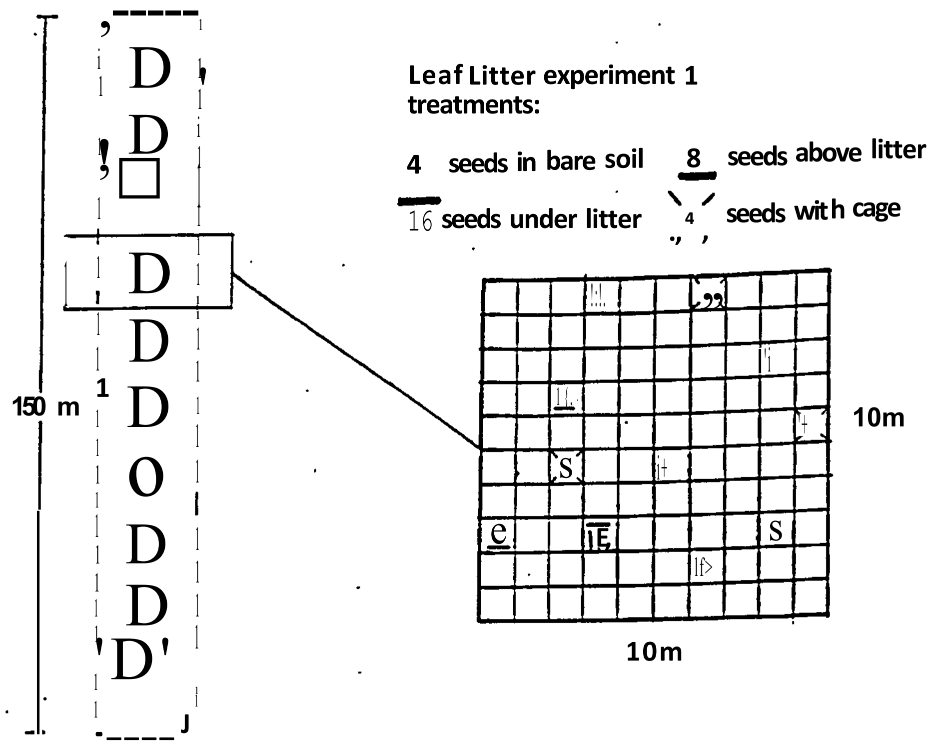
Astrocaryum

Variable	Parameter Estimate	Standard Error	Wald $x2$	Standardized Estimate	Prob. $x2$
Intercept	2.9957	0.7246	17.094	.	0.0001
litter	-1.6433	0.7803	4.435	-0.4381	0.035

Dipteryx

Variable	Parameter Estimate	Standard Error	Wald $x2$	Standardized Estimate	Prob. $x2$
Intercept	0.5008	0.2834	3.122	.	0.077
litter	-0.3185	0.3920	0.660	0.4165	0.088

Figure 1. Experimental designs of field experiments 1 and 2, in which I investigated the effects of the presence of leaf litter on ***Astrocaryum*** and ***Dipteryx*** seed survival. ln experiment one, 10 x 10 m blocks with the experimental treatments were replicated ten times within the 150 m transect. Each block was subdivided into one hundred $1m^2$ sub-plots. Numbers within the cells represents the seed number used. Within blocks, each seed number was replicated four times, one replication per leaf litter treatment. Thy position of the seeds was assigned by using a random number table. To simulate natural conditions, the design was used for ***Astrocaryum*** and ***Dipteryx*** seeds separately. ***Dipteryx*** seeds were placed in a similar arrays, and in the sarne experimental blocks, but about 2 months later and one week after ali ***Astrocaryum*** seeds had been predated in the sarne experimental blocks. ln experiment 2, only ***Astrocaryum*** seeds were used, and only one seed number was used. The number and size of blocks used were the sarne as in the first experiment. The black fi11 covering the subplots represents the portions of the $1m^2$ plots covered by litter. A11 treatments had eight seeds, and each litter treatment was replicated four times within each of the ten blocks. See methods for further details.


Leaf Litter experiment 1
treatments:
4 seeds in bare soil
8 seeds above litter
16 seeds under litter
4 seeds with cage
150 m
10m
10m

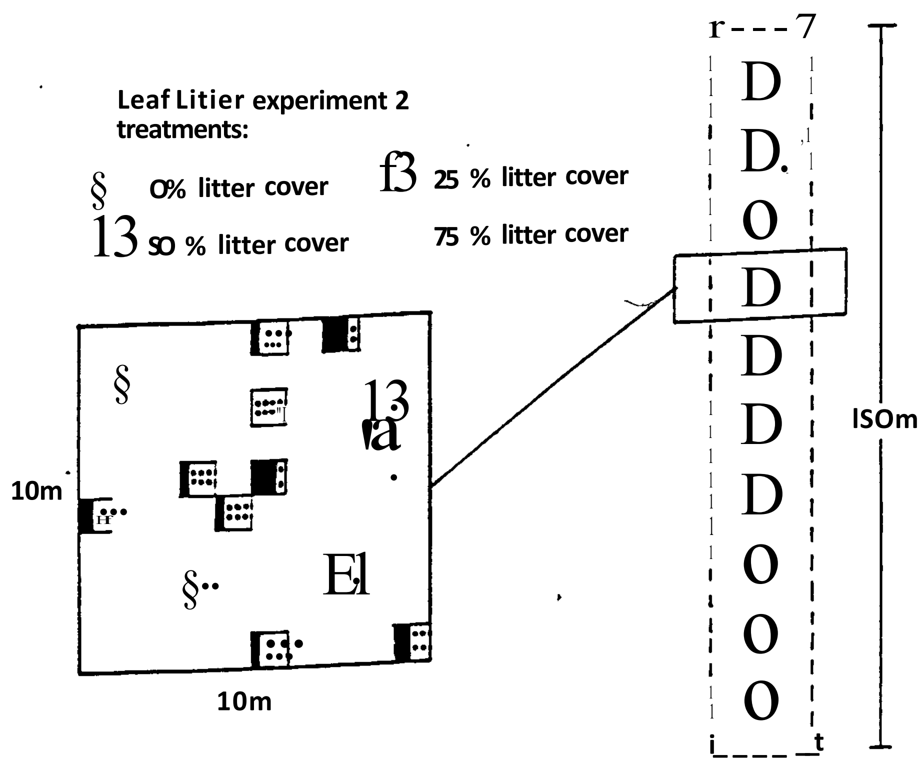
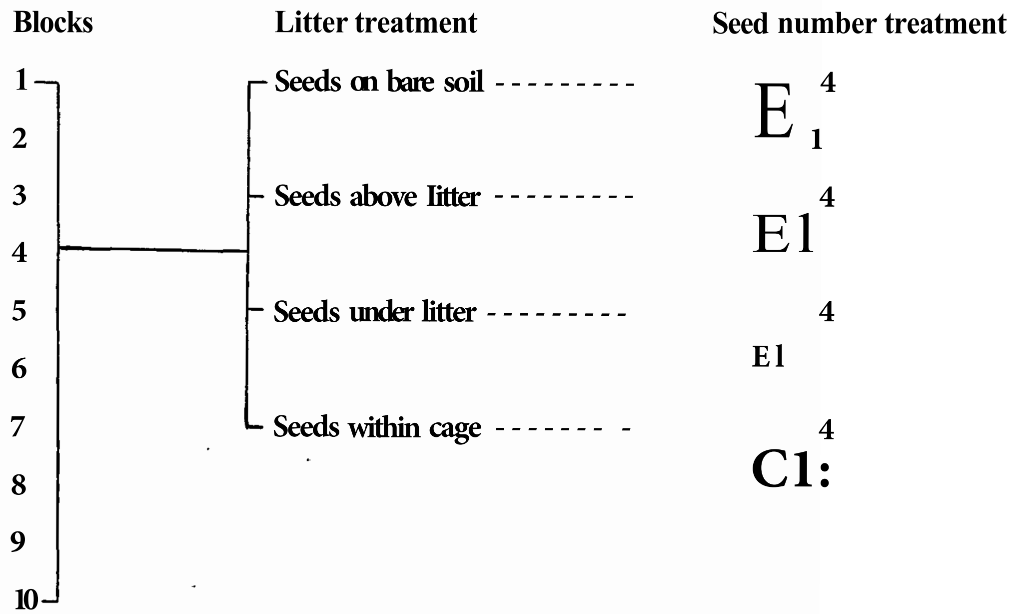

Leaf Litier experiment 2
treatments:
0% litter cover
25 % litter cover
50 % litter cover
75 % litter cover
10m
10m
150m

Figure 2. a. Design used for litter experiment 1 for *Astrocaryum* and *Dipteryx* seeds. Experiments were conducted at different periods for each plant species. b. Design used in for litter experiment 2 in which only 8 *Astrocaryum* seeds were used in each replicate. See methods for more details.

a. Design of the Leaf Litter experimet 1 *(Astrocaryum* and *Dipteryx* seeds were used)



b. Design of the Leaf Litter experimet 2 (only *Astrocaryum* seeds were used)

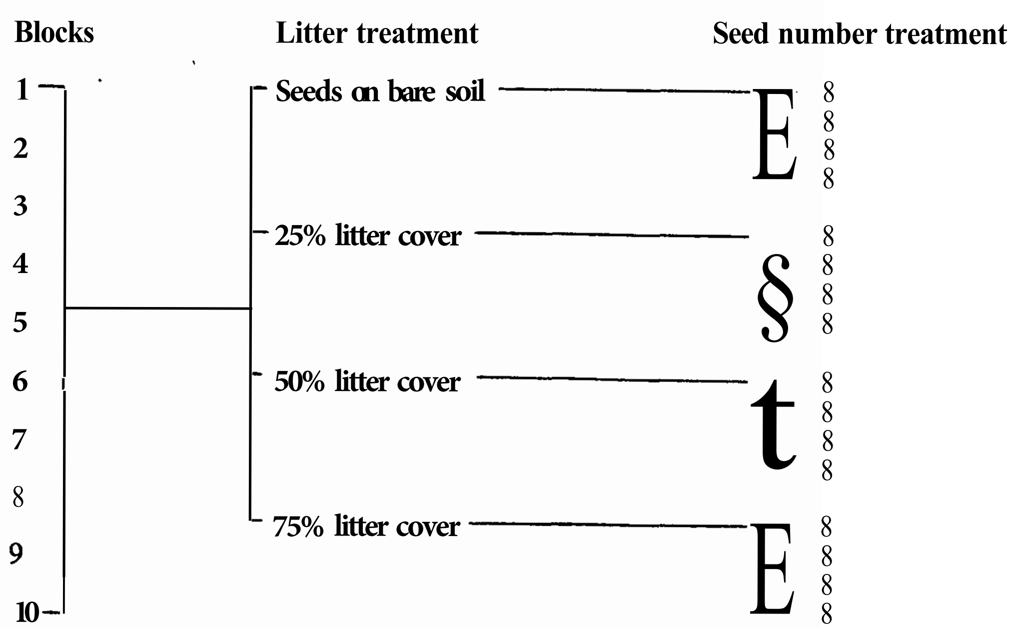
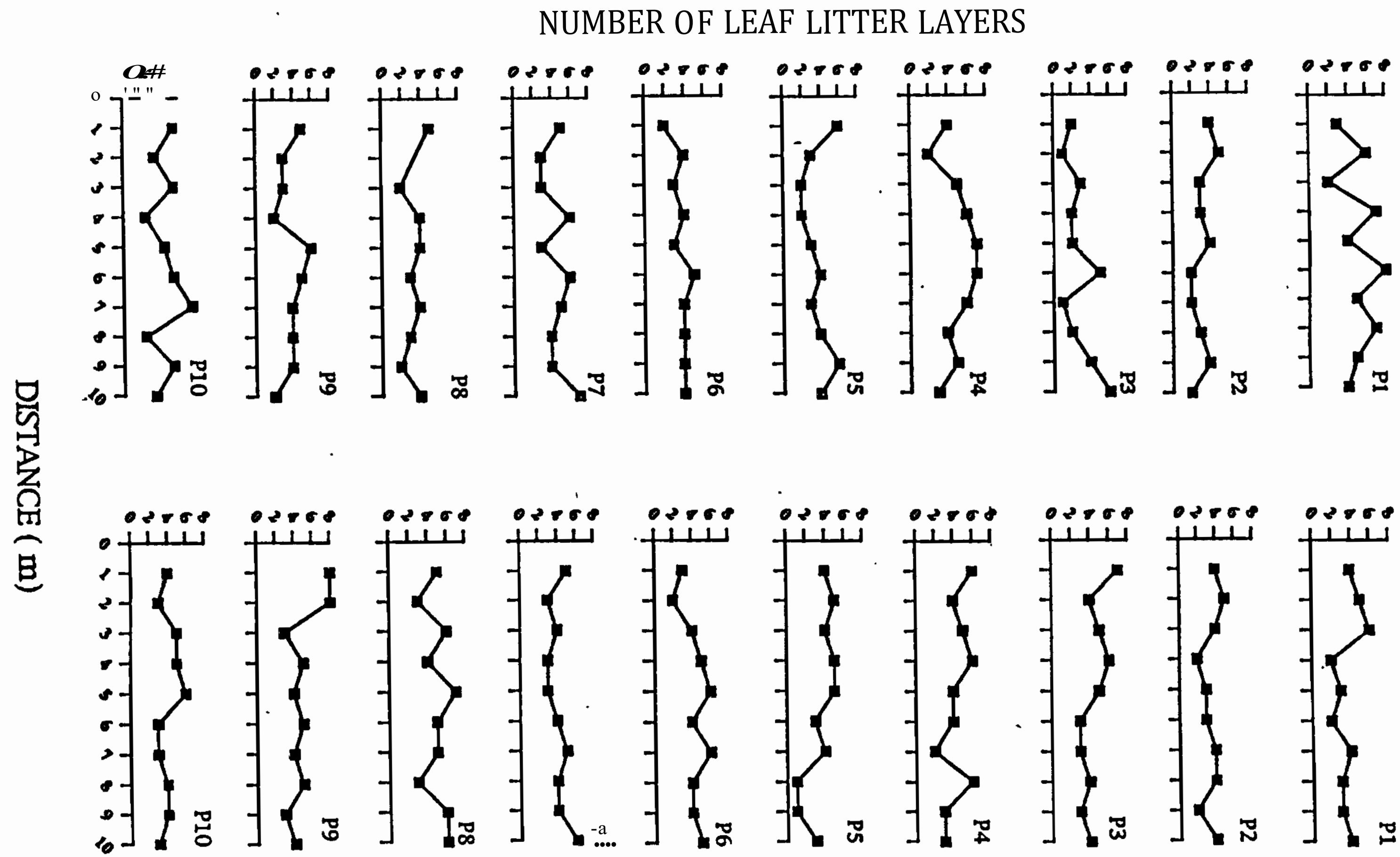


Figure 3. Spatial variation in leaf litter thickness in relation to distance (meters) within each 10 x 10 m plot (Pl to PlO) (measurements were taken along the egde of the plots) located along 150 m transects at the sites where experiments 1 (left graphs) and 2 (right graphs) were conducted.



NUMBER OF LEAF LITTER LAYERS
DISTANCE (m)
P1
P2
P3
P4
P5
P6
P7
P8
P9
P10

Figure 4. Survival functions for seeds in litter experiment 1, in which I investigated *Astrocaryum* seed survival in relation to three "seed number treatments" (4, 8 and 16 seeds/m^2 and their location in three "litter treatments" (seeds on bare soil, under and above litter). The ordinates represents the proportion of the original population of seeds that was still present at the start of each weekly census interval. *Astrocaryum* seed survival was significantly lower in microsites with bare soil than in those covered by litter (upper graph). *Astrocaryum* seed survival did not differ with seed number (lower graph). Initial seed survival of *Astrocaryum* seeds was highly different between litter treatments ("Wilcoxon test", x2 = 63.2, DF=2, p=1.86e-14). Differences between treatments in late seed survival were highly significant as well ("Log Rank test", x2 = 102, DF=2, p=0.0000. Seed number treatments also showed significant differences in early seed survival ("Wilcoxon test", x2 = 6.4, DF=2, p=0.040). Differences between leaf litter treatments on late survival were also highly significant ("Log Rank test", x2 = 11.9, DF=2, p=0.002).

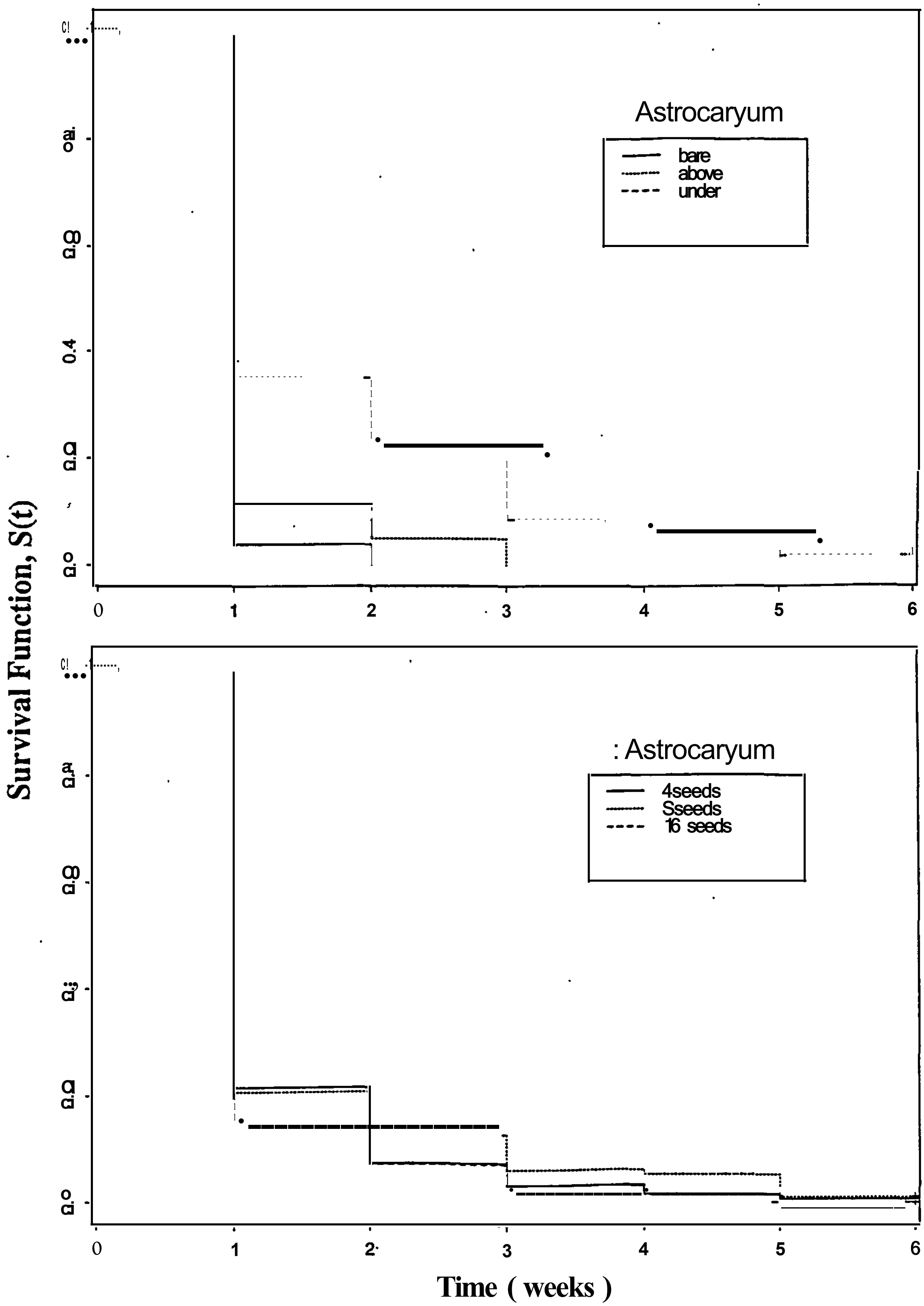

Astrocaryum
bare
above
under
Astrocaryum
4seeds
Sseeds
16 seeds
0
1
2
3
4
5
6
Survival Function, S(t)
Time (weeks)

Figure 5. Survival functions for seeds in litter experiment 1, in which I investigated *Dipteryx* seed survival in relation to three seed number treatments (4, 8 and 16 seeds/m^2 and their location in three litter treatments (seeds on bare soil, under and above litter). The ordinates represents the proportion of the original population of seeds that was still present at the start of each weekly census interval. *Dipteryx* seed survival was significantly lower on top of litter and on bare soil than when the seeds were covered by litter (upper graph). Seed number treatments were not significantly different (lower graph). Initial seed survival of *Dipteryx* seeds was highly different between litter treatments ("Wilcoxon test", $X2 = 92$, DF=2, p=0.0000). Differences between litter treatments in late seed survival were highly significant as well ("Log Rank test", x2 = 98.5, DF=2, p=0.0000). Seed number treatments showed significant differences in early seed survival ("Wilcoxon test", $X2 = 12.7$, DF=2, p=0.001). Differences between seed.number treatments on late survival were also significant ("Log Rank test", x2 = 8.6, DF=2, p=0.01).

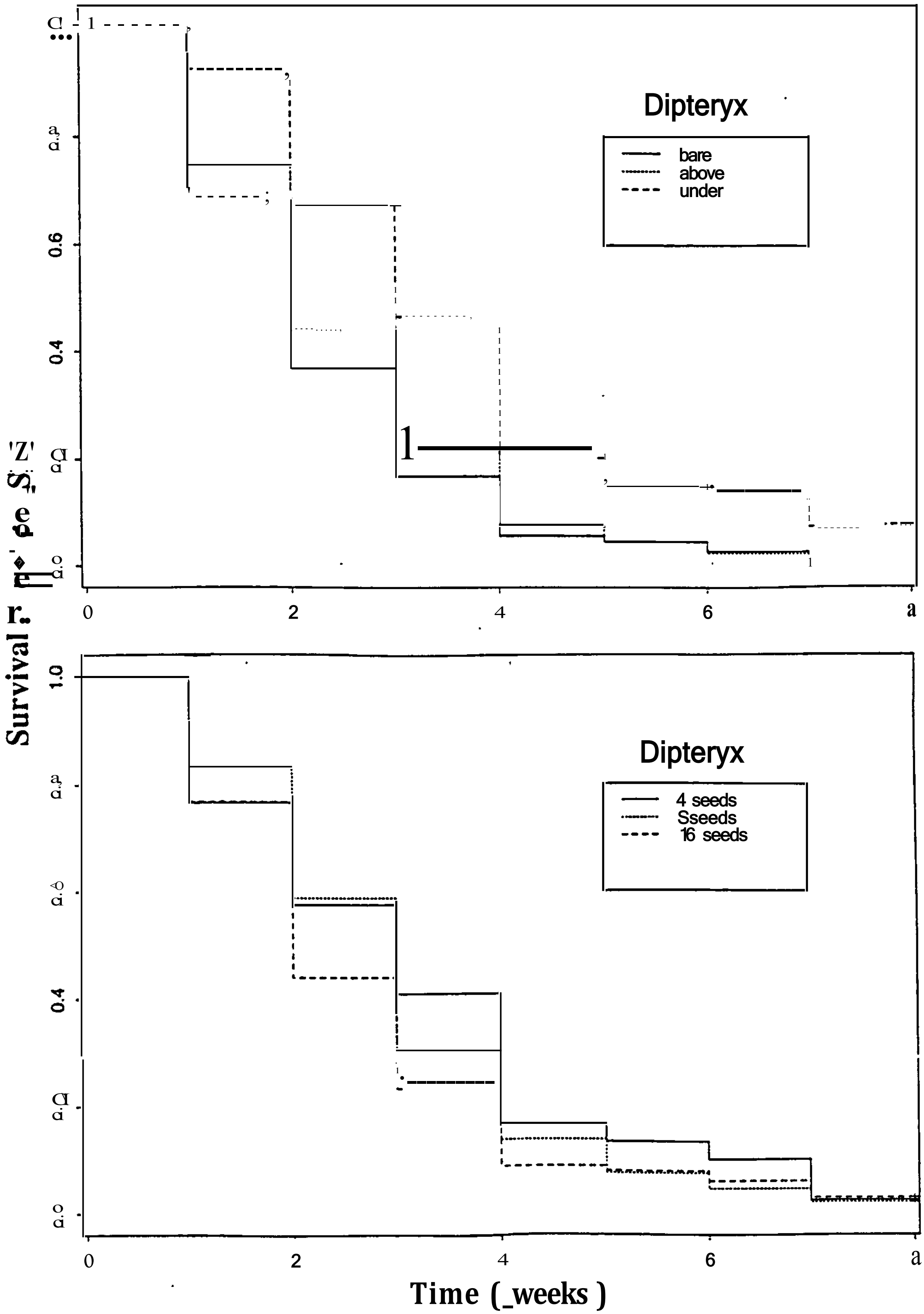

Dipteryx
bare
above
under
Dipteryx
4 seeds
Sseeds
16 seeds
Survival
Time (_weeks)
0
2
4
6
0.6
0.4
1.0

Figure 6. *Astrocaryum* and *Dipteryx* seed survivorship descriptive results from experiments 1 and 2, in which I analyzed the effects of leaf litter on seed survival. Toe columns in the two graphs on the left are means ± standard error of "time 50% seed survival (weeks)" for *Astrocaryum* seeds (upper graph) and *Dipteryx* seeds (lower graph).

Toe columns in the two top graphs on the right represents means ± standard error of "maximum seed survival time (weeks)" for both plant species. Toe four experimental treatments used in experiment 1were: (1) seeds placed in bare soil, (2) seeds placed above litter, (3) seeds placed_under litter, and (4) seeds protected by the hard wire mesh cages.

Toe lower graph on the right is the result from the experiment 2, in which I investigated how *Astrocaryum* seed survival survived under litter protection at diffreent spatial scales (areas of the experimental plots covere by litter. Toe columns are the means ± standard error of the "maximum seed survival times (in weeks)" under the following four leaf litter treatments: (1) seed placed in $1m^2$ plots with bare soil (0% of litter cover), (2) seeds placed in $1m^2$ plots with 25% of the plots area covered by litter, (3) seeds placed in $1m^2$ plots with 50% of the plots area covered by litter, and (4) seeds placed in $1m^2$ plots 75% of the microsites covered by litter.

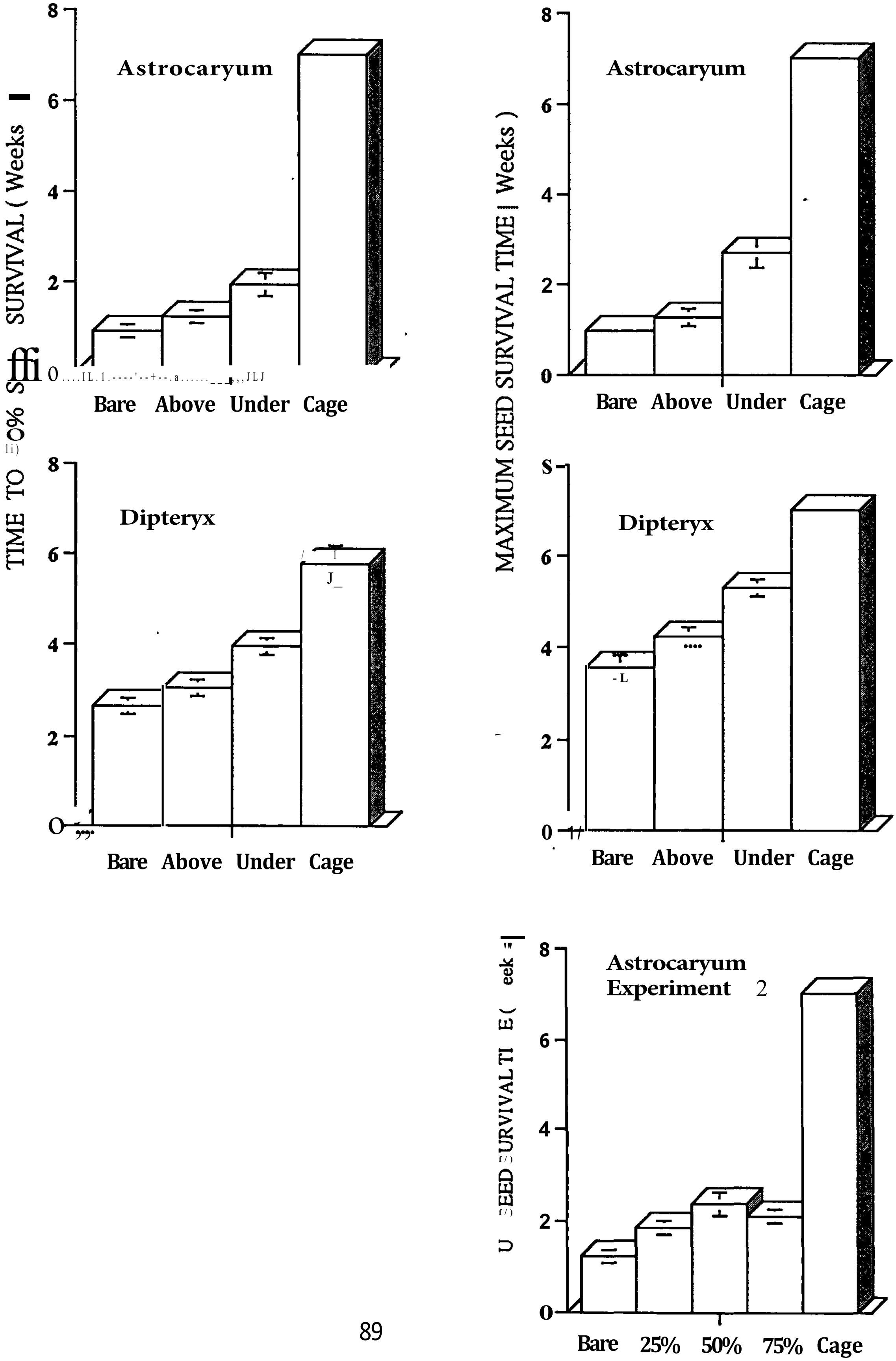
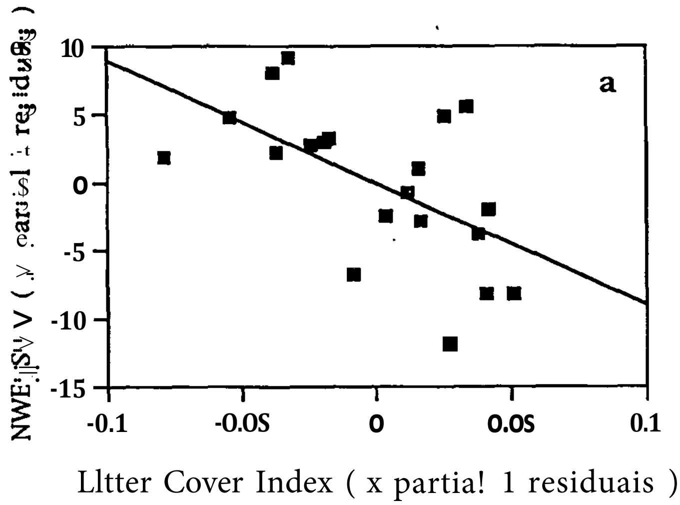
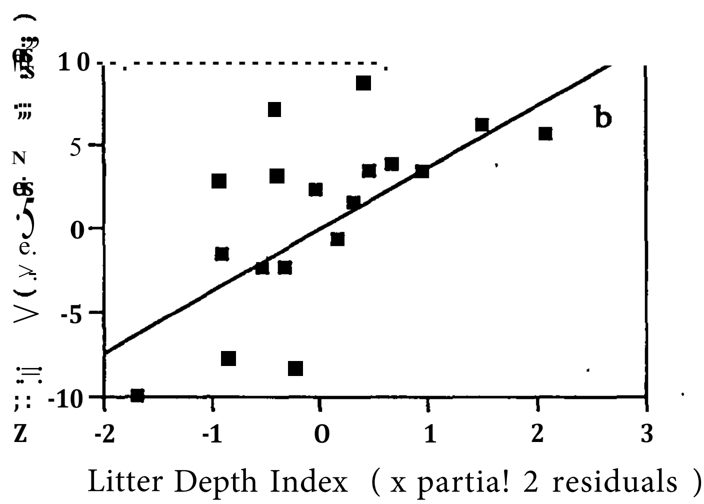
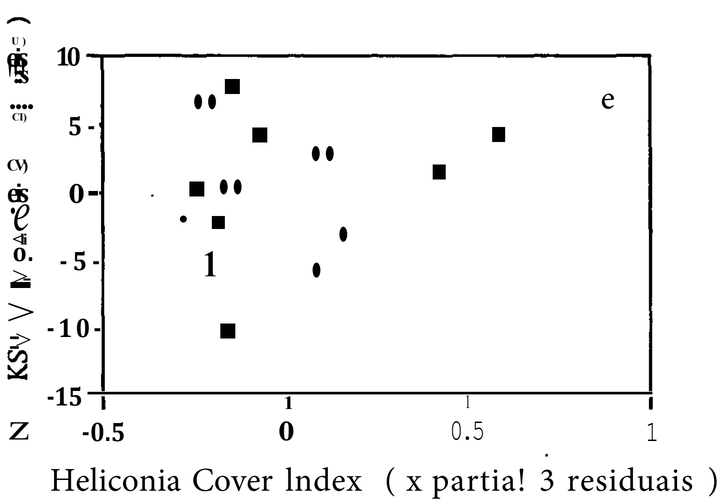

TIME TO 50% SURVIVAL (Weeks)
Astrocaryum
Dipteryx
Bare
Above
Under
Cage
MAXIMUM SEED SURVIVAL TIME (Weeks)
Astrocaryum
Dipteryx
Bare
Above
Under
Cage
Astrocaryum
Experiment 2
Bare
25%
50%
75%
Cage
0
2
4
6
8

Figure 7. Partial regression plots of the residuals of the response variable, " proportion of ***Astrocaryum*** seeds surviving" against the residuals of each of the independent variables: (a) litter cover index; (b) litter cover depth; (e) ***Heliconia*** cover index; (Residuals for each of the three plots come from the multiple regression analysis of Table 6).


a
10
5
0
-5
-10
-15
-0.1
-0.0S
0
0.0S
0.1
Lltter Cover Index (x partia! 1 residuais)


b
10
5
0
-5
-10
-2
-1
0
1
2
3
Litter Depth Index (x partia! 2 residuals)


e
10
5
0
-5
-10
-15
-0.5
0
0.5
1
Heliconia Cover lndex (x partia! 3 residuais)

Chapter 3

THE JANZEN-CONNELL MODEL AND PLANT DIVERSITY IN THE TROPICS: A CASE STUDY OF TWO COMMON AMAZONIAN TREE SPECIES IN THE AMAZON FOREST.

Summary

Tropical biologists have proposed severa! interesting models to explain the mechanisms that maintain the high tree species diversity in tropical forests. The Janzen-Connell model (Janzen 1970, Connell 1971), assumes that the concentrated action of seed and seedling predators near fruiting trees results in higher mortality of offspring close to parent trees. Therefore, seedlings may not often establish in the immediate vicinity of parent trees. Seedlings of other species may thereby have opportunities to occupy the site, and maintain local plant diversity. ln this study I used factorial experiments and the technique of survival analysis to investigate whether this model was operating for two common Amazonian tree species: the midstory palm, *Astrocaryum murumuru*, and the canopy emergent legume, *Dipteryx micrantha.*

Seed and seedling survivorship pattems *of Astrocaryum* supported the Janzen-Connell model. *Astrocaryum* seed predation by insects and mammals was density-dependent A higher proportion of *Astrocaryum* seedlings survived farther than close to adult trees. *Dipteryx* seed survival increased with distance from an adult, ;md was negatively related to the number of individuals present in clumps of adult trees. Pattems of seedling survivorship in both species were dependent on spatial scale and year. Se d and seedling predators may help to maintain the local tree diversity by suppressing the

recruitment of conspecific juveniles around adults, thereby creating opportunities for other plant species.

Introduction

Toe mechanisms that maintain high tree diversity in tropical forests have long fascinated biologists (Wallace 1878). Since the 1930s, the effect of distance from parent trees on seed and seedling mortality has been postulated as fundamental to maintaining the higher plant diversity of tropical forests, as compared to that of temperate forests (Ridgley 1930).

Toe best known model assumes that density-responsive predators and pathogens tend to concentrate near parent trees (Janzen 1970, Connell 1971). Here they impose high seed and seedling mortality. Propagules dispersed far from the mother plant will. escape predation and thus enjoy higher survivorship. Peak recruitment may therefore occur at some distance away from, rather than beneath, the mother plant. ln tum, propagules of other plant species will colonize the "empty" space around the focal tree, thereby maintaining plant diversity. Howe and Smallwood (1982) have called this the "escape hypothesis".

Although density and distance effects on seed and seedling survival have been the focus of about 50 studies in the tropics (see review in Clark and Clark 1984, Clark 1986, Connell et. al. 1984, Schupp 1988, Howe 1991, Forget 1992, Terborgh et al. 1993), the relative importance of these effects for individual trees and their population biology remains controversial because of the many studies which results supported predictions from Janzen-Connell model and other studies did not (Janzen 1969, 1970, Connell 1971, Hubbell 1979, 1980, Becker et al. 1985, Fenner 1986, Murray 1986, Estrada and Fleming 1986, Wilson 1988, Howe 1991, Condit et al. 1992).

Much of the emphasis in testing this hypothesis has been on analysis of spatial pattems of survival of dispersed seeds during one time period, the pre-germination phase. Toe static mapping of older saplings and juvenile trees does not provide a direct test of the Janzen-Connell model, because it ignores the possibility of change in spacing pattems dueto temporal changes in the survival of seedlings (Augspurger 1983).

The relative spatial scales on which density and distance effects may operate has only recently been investigated (Andersen 1989, Schupp 1992).

At Cocha Cashu Biological Station in the Peruvian Amazon, the palm *Astrocaryum murumuru* (Mart.) and the legume *Dipteryx micrantha,* are relatively common and regarded as keystone species, because they support many vertebrates during annual periods of food scarcity (Terborgh 1986). These two large-seeded tree species share similar seed dispersers and predators, and seedlings can be observed throughout the forest Although *Astrocaryum* and *Dipteryx* could be called shade tolerant (sensu Swaine and Whitmore 1988), seedlings of both species establish not only in the understory, but also colonize small to medium-sized gaps and the peripheries of large gaps (Bonaccorso et al. 1980, Smythe 1989, Forget 1993, Terborgh et al. 1993). However, the population structure of these tree species are markedly different (see chapter 1).

As part of a long-term study of the demography of these two species at Cocha Cashu, I conducted experiments to investigate which biotic and abiotic factors most affect seed and seedling survival. In this chapter, I test the escape hypothesis for *Astrocaryum murumuru* and *Dipteryx micrantha* and investigate the circumstances under which it applies to these species. I also investigated whether the mechanisms predicted by the

Janzen-Connell model were operating for these two plant species. I used methods similar to those being used in other tropical regions to facilitate comparison.

I monitored the survival of naturally occurring seeds and seedlings, as background to a series of experimental manipulations. Toe questions I asked were: 1) Are *Astrocaryum* and *Dipteryx* seed and seedling survival affected by local abundance of conspecific seeds, seedlings and adult trees ? 2) Are *Astrocaryum* and *Dipteryx* seed and seedling survival dependent on distance from parent trees? 3) How does seed survival vary in the vicinity of dumps of few, more, and many adults?

CHARACTERISTICS OF THE STUDY AREA - Toe research was conducted between August 1991 and June 1993, at the Cocha Cashu Biological Station, Manu National Park, Madre de Dios, Peru. Toe research station and surrounding forest lie in the floodplain of the Manu River. Annual rainfall there is approximately 2000 mm, and mean annual temperature is about 24 °c. An annual dry season extends from May or June through October, and a wet season follows from November to May. Toe forest has many emergent trees anda complex vertical structure (Terborgh and Petren 1991). Information on the local plant and animal communities is summarized in Gentry (1991).

BIOLOGY OF *Astrocaryum murumuru* and *Dipteryx micrantha*

Information on the biology of *Astrocaryum* and *Dipteryx* at Cocha Cashu was presented in Chapter 1.

Methods

This chapter is divided into two parts. In the first, I describe three experiments in which I analyze the survival of experimental seeds in relation to clumping, distance from adult trees, clumping of adult trees, and the impact of insects and mammals on seed mortality. In the second part, I analyzed the mortality over a 1-year period of naturally occurring seedlings in relation to their density and distance from adult trees.

EXPERIMENT 1: SEED SURVIVAL INRELATION TO SEED NUMBER AND DISTANCE FROM ADULT TREES.

The purpose of this experiment was to evaiuate the effects of seed density and distance from parent tree on seed survival.

EXPERIMENTAL DESIGN To examine how dista'lce from an adult tree might affect *Astrocaryum andDipteryx* seed survival, I used the following three treatments around 10 focal adult *Astrocaryum* and 5 focal adult *Dipteryx* trees : 1) seeds under the focal tree, close to the trunk; 2) seeds at 5·m *(Astrocaryum*) and 10 m *(Dipteryx)* from the focal tree; and 3) seeds at 20 m *(Astrocaryum*) and 40 m *(Dipteryx*) from the focal tree (Figure 1). The outer distances used for the two species maintained a rough proportionality of three times the respective crown radius of the two species.

Adult *Dipteryx* trees were located within 50 m on either side of a trail over the whole Cocha Cashu floodplain. (about 200-400 ha). Focal trees were then selected on the map. *Astrocaryum* trees were selected along the trail, with the distance values being chosen from a random number table. To assure the independence of replicates, I selected relatively isolated focal trees, those located more than 50 m from any conspecific. Also focal trees were located 100-200m from one another.

Experimental seeds were set out along transects radiating along the four cardinal directions from the trunks of focal trees (Figure 1). Experimental seeds were set out in groups of 4, 8 and 16, covering the range of numbers seen in bat roosts and rodent catches in the study area (Pers. Observ). Seed groups of 4, 8, or 16, were organized in plot sequences along the transects (See Figure 1). Experimental seeds were evenly arrayed within each plot.

I used thirty-six 30 x 30 cm experimental plots per focal tree, resulting in 4 replicates of each seed number treatment per distance treatment. The entire experiment deployed 360 plots containing ***Astrocaryum*** seeds and 180 plots containing ***Dipteryx*** seeds, for a total of 3360 ***Astrocaryum*** and 1600 ***Dipteryx*** seeds (Figure 1).

As a control, I recorded the number of seeds already present under the focal trees, (hereafter called natural seeds) in five randomly located 30 x 30 cm plots under each ***focalAstrocaryum*** tree in the study. I found so few naturally occurring seeds near adult ***Dipteryx*** trees that I did not follow their survival. Natural seeds were censused weekly for 20 weeks along with experimental seeds. I used colored tooth picks to mark the positi.ons of plots with experimental and natural seeds (see below).

I also wanted to have a rough estimate of the number of seeds already present on the forest floor beneath adult trees in the study area. Therefore I surveyed the number of seeds within 2 m of the trunk of another 20 ***Astrocaryum*** trees within a 2.5 ha plot. I also recorded the numbers of seeds under a number of ***Dipteryx*** trees located far from the focal trees.

ln Experiment 1, I used 336 seeds/focal tree to approximate the number of seeds found in these surveys. Once a week, I searched for displaced seeds (within a radius of 3-

5 m of each group of experimental seeds) to determine their fate. The survival of experimental seeds was followed for either ten weeks or until all died or disappeared. STATISTICALANALYSIS- I conducted survival analyses using the Cox Proportional Ha.zaid Regression model procedure available in Splus (1991). This procedure combines repeated censuses into a single test, and correctly incorporates right-censored data (i.e. those seeds still surviving at the end of the experiment for which survival times are not known). Toe Cox mod.el calculates the parameter "survival function," a survivorship curve, which represents the proportion of the initial seed population still present at each successive census (Cox and Oakes 1984).

Toe *Astrocaryum* -experiment was initiated one month ahead of the *Dipteryx* experiment in accord with their respective phenologies. Cox Proportional Hazard Regression was fitted to the seed survival distribution separ tely for each plant species. Two additional tests were used to compare survival functions (equality of survival curves) among the seed number treatments: the Mantel-Haenzel test (Log-Rank test), and Peto-Peto's test (a modification of the Gehan-Wilcoxon test) (Splus 1991). I used both tests because the former emphasizes late .survival while the latter gives greater weight to early survival (Splus 1991). For more examples of ecological studies using survival analysis see Pyke and Thompson (1986), Schupp (1990), and Dixon anctNewman (1991).

I also investigated the impact of seed predators in relation to the initial size of the seed number treatments. ln this analysis, the response variable for both tree species was the time to 50% seed loss. I used this response variable because V3J?-ation in the numbers of seeds in the groups was greatest initially.

To analyze seed survival in relation to seed number and distance from focal adult trees, I used a fully crossed factorial ANOVA (GLM-SAS 1987). Toe response variable used was the" number of weeks to 50% seed survival." I tested for possible differences in seed survival between focal trees, between distances (O, 5-10, and 20-40m from the focal trees), and between seed number treatments (4, 8 and 16 seeds/plot), along with the respective pairwise combinations of interactions among these three variables (second level), and the interaction among all of them (third leve!).

A bias in the factorial ANOVA could enter as a result of time-varying numbers of seeds in the seed number treatments. To address this possibility, I used the weight statement available in MGL-SAS for variable "seed numbers" and ran the sarne factorial ANOVA's (one for ***Astrocaryum*** and one for ***Dipteryx)*** using the the response variable "number of weeks to 50% seed survival." The results were similar. This indicates that the weights of the observations (seed number) were proportional to the reciprocais of the error variances, and that the weighted least-squares estimates were best linear unbiased estimators.

EXPERIMENT 2: SEED SURVIVAL IN RELATION TO THE NUMBER OF ADULT TREES IN DIFFERENT-SIZED GROUPS OF TREES

Hubbell (1979) showed that most tree species in a tropical forest have clumped distributions. Therefore, differences in the size of clumps of adult trees may affect spatial regeneration dynamics within the forest by creating environmental heterogeneity at larger scales. This experiment was conducted to investigate whether it is advantageous for trees of both species to have their seeds dispersed to small vs large stands of adult trees (see below). The experiment was conducted on a larger spatial scale than experiment 1 (within an area of 50-100 ha). Seed survival was determined in relation to the size of clumps of adult trees. I also wished to investigate whether vertebrate seed dispersers and predators tend more often to visit the larger *Astrocaryum* and *Dipteryx* stands in the forest.

EXPERIMENTAL DESIGN - Twelve groups of adult trees (six groups of *Astrocaryum* and six of *Dipteryx)* were used for this experiment. Groups of one, three, four, six, n. and thirteen adult trees were used. These groups of adult trees were located in a larger area (50-100 ha) than the focal trees of first experiment. Groups of *Dipteryx* trees were selected from the sarne map mentioned in experiment 1. Groups of *Astrocaryum* trees were also chosen following the sarne criteria as in the experiment 1, but differing in the distances between groups of trees. All tree groups were more than 200 m apart, except the groups of 4 and 10 *Astrocaryum* trees which were less than 100 m apart.

ln each group, two trees at least 30 m apart were selected as target individuais around which experimental seeds were placed (see Figure 2). At each of the two selected trees withineach stand, 32 seeds were set out on the leaf litter: 16 seeds under the crown of the 'target' tree and 16 seeds away from the 'parent trunk (20 m for *Astrocaryum* and 40 m for *Dipteryx*).' Each seed position had two seeds separated by 20 cm; one carried a "tail flag" and the other did not (the "tail" being a 20 cm long piece otmonofilament fishing line linked to a 10 cm long pink plastic lace attached to a 1 cm long numbered plastic tag). I also marked each seed with an individual number protected with a coat of waterproof glue.

STATISTICAL ANALYSIS-ln this part of the study, linear regression (MGHL- S.ystat, Wilkinson 1991) was used to test: 1) how seed survival is related to the number of trees in clumps of adults with different numbers of trees; 2) whether variation in the natural densities of seeds beneath individual trees in the experimental groups of trees was related to the survival of seeds.

EXPERIMENT 3: THE IMPACT OF INVERIBBRATE AND VERIBBRATE SEED PREDATORS ON SEED SURVIVAL AT SMALLER SPATIAL SCALES

Astrocaryum seeds at Cocha Cashu are attacked by both insects and mammals (Terborgh et al. 1993). I analyzed the relative impacts of insect and mammalian predators on seed mortality in relation to seed density and size of the groups of adult trees at this time within a much smaller area than those used for experiments 1 and 2.
I analyzed the conclitions of naturally occurring seeds within a 1-2 m raclius around the trunks of 20 adult palms, all located within a 2.5 hectare plot (a much smaller spatial scale than that used in the experiments 1 and 2). There were four *Dipteryx* trees within the plot and 36 *Astrocaryum* trees. Therefore, only *Astrocaryum* trees were used. Also, in this analysis, I separated the impact of insects from that of mammals on *Astrocaryum* seed survival, to determine whether predation was dependent on seed density and number of *Astrocaryum* trees in a given forest patch.

Seeds were collected between the 17th and 22nd of August within a raclius of 2 m around the trunks of 20 adult trees located in clifferent-sized groups of *Astrocaryum* trees within the 2.5 ha plot. Seeds were counted, stored in plastic bags, and identified by the plot number and number of the adult tree from which they were collected. Undamaged seeds were washed and dried carefully in the laboratory before opening.

I first examined each s for external signs of predation by a mammal (1/3 to half of the seed shell typically destroyed), or an insect (small boles ranging from 1 to 3 mm cliameter, and presence of larval and/or adult beetles within the seeds). I also broke undamaged seeds with a hammer and recorded whether the seed had been invaded by insects or was viable.

I set up four random 30 x 30 cm plots around each of 20 adult palm trees within the 2.5 ha plo,t. I then collected all *Astrocaryum* seeds within the 30 x 30 cm plots, and analyzed their conclitions (see paragraph above). Within the 2.5 ha plot, the adult trees were located in groups of 1, 2, 3, 4, 5, 6, 7, 13, and 14 trees. Except for a 'group' with one tree, seeds were collected from two adult trees in each group. Toe adult trees from which I collected the seeds were located at the periphery of the respective tree cluster, and at least 20 m from selected adult trees in the other groups.

STATISTICAL ANALYSIS- ln the third experiment in which seed mortality is analyzed on a larger scale (within the 2.5 ha plot), multiple regression models (MGLH-SYSTAT, Wilkinson 1992) were used to investigate whether seed predation by insect and mammalian herbivores (response variables) were dependent on seed density and on the size of clumps of adult trees (independent variables).

Here I shall use the term "seed" to refer to a hard endocarp containing a seed because it is in this form that the progagules of *Astrocaryum* and *Dipteryx* are dispersed in nature. I collected seeds for the experiments at the beginning of June 1992, which was the first week of the *Dipteryx* fruiting period that year. Collected seeds were pooled and then washed and dried in the sun for about two hours. Only intact seeds were used in the experiments.

To investigate secondary dispersai clistances and the fate of àispersed seeds, I ran a pilot experiment in 1991 in which I attached small numbered magnets on 300 *Dipteryx* seeds, and subsequently tracked them with a magnetic locator. I found that 98% of the seeds that had been removed were preyed upon by mammals (rodents). Thereafter, I considered that clisappearance of a seed was equivalent to predation. '.fhe experiments were run during the annual period of food scarcity during which *Astrocaryum* and *Dipteryx* seeds are portant food resources for many seed predators (Terborgh 1986).

SEEDLING SURVIVAL INRELATION TO SEEDLING DENSITY, DISTANCE FROM NEAREST NEIGHBOR, DISTANCE TO THE NEAREST CONSPECIFIC ADULT TREE ANO DENSITY OF CONSPECIFIC ADULT TREES.

To investigate and compare seedling survival in both plant species in relation to density and distance from the nearest adult tree, I subdivided the sarne 2.5 ha plot mentioned above into 1Ox 10 m subplots and I mapped all *Astrocaryum* and *Dipteryx* seedlings. I mapped seedlings to a precision of about 10 cm. Numbered aluminum tags were attached to each seedling. I followed seedling performance (growth and survival) by monitoring the plot five times between October 1991 and October 1993. By revisiting the plot 5 times, I was able to distinguish whether seedling mortality was due to predation or other abiotic and biotic factors. I used a program in Power Basic (1989) to calculate, for each individual seedling, the minimum distance to the nearest neighbor and to the closest adult tree within the 2.5 ha plot . The program also estimated seedling density by counting the number of seedlings within 5 m and 10 m annulus of each seedling. Adult tree density was measured by counting adult trees within 20 m around a target tree. Because there were only four adult *Dipteryx* trees in the plot, tree density was not considered in the analysis for this species.

STATISTICAL ANALYSIS- I investigated whether the survival of seedlings from both plant species was dependent on the distance to the nearest neighbor, seedling density, distance to the nearest adult tree, and density of adult trees I used these four variables in a logistic regression analysis in which seedling survival was used as the binary response variable (survival=l, mortality=O). I used the logistic procedure available in SAS (1987) to run this analysis. Seedling survival was analyzed for two different years (1992 and 1993), and for two different spatial scales (seedling densities within 5 and 10 m around each seedling) for each of the two plant species. For the logistic regressions, only those seedlings were used for which I had measurements of the four variables just mentioned; therefore, seedlings within 5 m and 10 m of the plot edge were not considered, respective to each spatial scale considered.

Results

EXPERIMENT 1: SEED SURVIVAL IN RELATION TO SEED NUMBER, DISTANCE FROM PARENT TREE, ANO NATURAL DENSITY OF SEEDS

Toe maximum time seeds survived at all seed densities and distances from 8 out of 10 focal trees, was about six weeks. Only two *Astrocaryum* trees had seeds surviving after ten weeks (end of the experiment), with 10-20% of the initial number of seeds from those trees surviving to that point ln the survival curves, the most critica! period of seed survival was between the first and third weeks, when 50% of the seeds were taken by predators (Figures 3a and 4).

ln the case of *Dipteryx*, seed loss reached 50% between the third and fifth weeks in most replicates (Figures 3b and 5). At the end of the experiment (12 weeks) only 100 seeds (5.9%) remained out of ali replicates.

Astrocaryum seed survival depended on seed number, but not distance. Seed survivorship was significantly higher in groups of 4 seeds than in groups of 8 and 16 seeds. Seeds placed 20 m from the tree trunk had no higher chances of survival than those placed close and at zero and 5 m from the trunk. Differences in seed survivorship among target trees were highly significant, indicating that seeds are taken by predators much faster around some trees than others (fable 1 and 2).

Dipteryx seed survivorship followed a different pattem from that of *Astrocaryum.* *Dipteryx* seed. survivorship was higher for seeds placed at 40 m than at 10 m from target trees, indicating a distance effect. Like *Astrocaryum* , *Dipteryx* seed. survival was significantly different among experimental trees (Table 1 and Figures 3b and 5). However, _*Dipteryx* seed survival did not depend on seed number.

With respect to initial conditions, there were significant differences in "time to 50% seed survival" between the two plant species (Table 2). No distance effects were detected around any of the target trees of either plant species (Table 2). Seeds placed on the litter close to the trunk, under the edge of the crown (5-lOm), and away from the target tree (20-40m), reached 50% mortality at similar times. There were no significant effects of seed number on seed survival (Table 1).

Because I recorded and followed the survival of seeds at the natural densities already present under *aduitAstrocaryum* trees (see methods), I could explore whether differences in seed survival between parent trees were due to variation in the natural seed density. I ran simple regression analyses, using the mean number of weeks to 50% seed survivorship as the response variable and the mean of the natural seed density from the *5* plots (see methods) under the parent trees as the independent variable. However, I counted natural densities of seeds only within 2 m radius around the *Astrocaryum* trunks. Therefore, I tested the effects of natural seed density on seed survival only under the target trees. For naturally occurring seeds, there were no effects of seed density on survivorship under target trees ($r=0.179$; $DF=8$; $F=0.266$; $p=0.620$).

EXPERIMENT 2: SEED SURVIV AL 1N RELATION TO TIIB NUMBER OF TREES 1N CLUMPS OF ADULTS 'IREES

Different patterns were found for swvival of *Astrocaryum* and *Dipteryx* seeds near different-sized clumps of adults. Seeds were predated by mammals in an equivalent way in clumps of adults of 1, 3, 4, 6, 10, or 13 trees. At the end of the dry season (November), there was no significant relationship between the number of seeds surviving under a parent tree and the number of *Astrocaryum* trees in clumps of adult trees (r=0.200; n=6; F=0.166; p=0.704). Nor was the number of *Astrocaryum* seeds surviving far from an adult affected by the number of trees in a clump (r=0.048; n=6; F=0.009; p=0.927). Toe total number of *Astrocaryum* seeds surv.iving was not related to the number of trees/clump. Also, for *Astrocaryum* , these results were not conditionally dependent on season.

There are no data for *Dipteryx* seeds for June. Survival of *Dipteryx* seeds under and far from parent trees in relation to number of trees/clump followed the sarne pattern as swvival of *Astrocaryum* seeds (for *Dipteryx* seed survival under a tree, r=0.673, n=6, F=3.307; p=0.143; and far from a tree, r=0.752, n=6, F=5.220, p=0.084). However, there was a negative and highly significant correlation between the total number of *Dipteryx* seeds surviving and the size of the clumps of adult trees (r=0.933; n= ; F=26.855; p=0.007, see also Figure 6).

EXPERIMENT 3: 1IIE IMPACT OF INSECT AND MAMMAL HERBIVORES ON *ASTROCARYUM* SEED SURVIVA L

In this experiment, I investigated survival of only *Astrocaryum* natural seeds. Both insects and mammals can attack *Astrocaryum* seeds. Therefore, I compared the relative impact of these two main predators types on seed survival in relation to seed density and size of the clusters of adult trees (in the 2.5 ha plot). I found a significant inverse relationship between predation by insects and seed density (Table 3 and Figure 7). Toe size of the clusters of adult trees also had significant inverse effects on *Astrocaryum* seed predation by insects (Table 3 and Figure 7).

Astrocaryum seed mortality caused by mammals was a positively and significantly correlated with seed density and not signifi.cantly related to the size of clumps of adult trees (Table 4 and Figure 7). I also counted the number-of seeds alive in the sarne 30 x 30 cm plots located within 2 m radius around each of the 20 *Astrocaryum* adult trees within the 2.5 ha, and ran the sarne analysis as above. Toe number of *Astrocaryum* seeds surviving was significantly related (Multiple Regression analysis $r2=0.639$, $p<0.028$, $DF=7$) to seed density ($T=3.14$, $p<0.01$), but not to size of clumps of adults ($T=1.831$, $p=0.110$).

EFFECTS OF DISTANCE TO THE NEAREST SEEDLING, SEEDLING DENSITY, DISTANCE TO CWSEST PARENT TREE AND DENSITY OF PARENT TREES ON *Astrocaryum* AND *Dipteryx* SEEDLING SURVIVAL.

Seedlings of both plant species were tagged within a 2.5 ha plot in 1991 to follow their survival for the next two years. All were naturally occurring seedlings. In 1992 *Astrocaryum* seedling density varied from 0.01 to 0.55 seedlings /m^2, and in 199j, 0.01 to 0. 2 seedlings /m^2. *Dipteryx* seedling densities range from 0.01 to 0.69 /m^2 in 1992, and 0.03 to 0.45 /m^2 in 1993. The density of *Astrocaryum* trees within the 2.5 ha plot varied from 0.007 to 0.072 trees /m^2.

In 1992, a higher proportion of *Astrocaryum* seedlings survived far from the adult trees, indicating escape in distance. This observed distance-dependent mortality was presumably dueto the action of herbivores such as deer and agouti (as the tooth marks on the cut seedling stems indicated) (Table 6). In 1993, *Astrocaryum* seedling survival apparently was not affected by any of the following factors: distance to the nearest seedling, seedling density (defined here as the number of seedlings within 5 m radius around each seedling), distance to the closest adult and density of adult trees (Table 6).

In 1992 *Dipteryx* seedlings were not affected by any of the factors mentioned above. However, in 1993, *Dipteryx* seedling survival was inversely related to the distance from adult trees. Significantly more *Dipteryx* seedlings survived beneath adult trees than further away (Table 6).

I also analyzed survival of *Astrocaryum* and *Dipteryx* seedlings at larger spatial scales such as 10 m radius around each seedling for seedling density for the sarne 4 factors. Under this spatial scale (10 m radius), *Astrocaryum* seedling survival (in both 1992 and 1993) was not affected by seedling density, nor by the distance to the nearest conspecific seedling, distance to closest conspecific adult tree or density of adult trees. Similar results were obtained for *Dipteryx* seedling survival in 1992. However, in 1993, higher *Dipteryx* seedling survival occurred beneath adult trees than in those farther away (Logistic regression, Wald Chi-square test=3.64, n=101, $p<0.05$).

Discussion and conclusions

THE EFFECTS OF SEED NUMBER ANO DISTANCE FROM PARENT 1REES ON SEED SURVIVAL

Toe escape hypothesis predicts that a disproportionally high seed mortality will occur in the proximity of adult trees due to attack by seed predators and pathogens, the impact of their activities being a positive function of seed density, and inversely related to distance from the parent tree (Janzen 1971, Connell 1971, Howe and Smallwood 1982). High mortality near the parent tree creates opportunities for other species to establish, and can help to explain tropical tree diversity.

An altemative model proposed by Hubbell 0980) predicts the reverse pattem. A small surviving percentage of a large number of seeds surviving beneath a parent tree could be larger than a higher percentage of a small number of survivin_g seeds dispersed away from the parent tree. Hubbell therefore concludes that unless mortality under the parent tree is nearly 100%, the population recruitment curve would peak beneath the parent tree. Toe expectation of this model is a clumped distribution of conspecific trees.

ln general, the findings of this study support the escape hypothesis (Janzen-Connell model). However, progeny survival depended not only on seed number and distance, but also on progeny age (seed or seedling), the kind of seed predators involved (insects or mammals), spatial scales on which the interactions of progeny with predators were analyzed, and year.

Toe results of experiment 1 showed no significant differences between survivorship of ***Astrocaryum*** seeds placed near the focal trees and seeds placed at distances up to 20 m from the focal trees, suggesting that for ***Astrocaryum,*** seed dispersai to 20 m from the parent tree does not help in escaping predation or enhancing seed survival. However, ***Astrocaryum*** seed survival, considering seed predation only by mammals, was positively dependent on seed number at both small and large spatial scales. This suggests that mammalian seed predators respond to variation in seed number in addition to presence in a given microsite on the forest floor.

On the other hand, ***Dipteryx*** seeds placed 40 m from parent trees survived longer than those placed beneath and at 10 m from an adult tree. Different results were found 10 years ago for ***Dipteryx panamensis*** at Barro Colorado Island (BCI) Panama, in which seed survival was equivalent for various distances up to 40 m from parent trees (De Steven 1984). However, additional results with ***Dipteryx panamensis*** at BCI showed higher seed survival at distances of 50 to 100 m, indicating positive distance effects on seed survival in this species (Forget and Milleron 1992).

At Cocha Cashu, ***Dipteryx*** seeds may show higher surorship beyond 40 m from parent trees, though Terborgh et al. (1993) found no distance effect at 50 m. However, it would be difficult to include 100 m from an adult as an experimental treatment and have enough replicates to test the escape hypothesis. This is because many adults in this population have a conspecific neighbor at distances less than 100 m. In this study, results from two independent experiments (1 and 3) confirmed that mammalian seed predation at Cocha Cashu is responsive to seed number. Because both ***Astrocaryum*** and ***Dipteryx*** fruit during the annual season of food scarcity it can be understood why more than 90% of experimental ***Dipteryx*** seeds and almost all ***Astrocaryum*** experimental seeds were taken by predators, with no spatial pattem in survival around the adult trees.

Significant differences in *Astrocaryum* and *Dipteryx* seed survival betwe_en focal trees were found in Ex.periment 1. Apart from the distance and seed number effects, *Astrocaryum* seeds had higher chances of survival in the pro:ximities of some trees than others (fables land 2). Recruitment within 20 m of an adult *Astrocaryum* tree, and 40 m of an adult *Dipteryx* tree may be a rare event in this forest, because almost all seeds had been -attacked by vertebrates by the end of the experiment

At smaller spatial scales, and with insect rather than vertebrate seed predators, the escape hypothesis may also be valid for *Astrocaryum* seeds. Similàr pattems of seed survival emerged for example, when seed predation was analyzed within the 2.5 ha plot (experiment 3). ln this spatial scale, *Astrocaryum* seed predation by bruchid beetles was density-dependent (fable 4). Seed predation by bruchids was also dependent on the number of adults in clusters of *Astrocaryum* trees (Table 4). Insect predation on *Astrocaryum* seeds had been found to show distance-dependence in a previous series of experiments in the sarne study area (ferborgh et al. 1993). Therefore, the Janzen-Connell model may be applicable for *Astrocaryum* seeds.

Predation by bruchids is very high on the seeds of other common palm species in the area, such as *Scheelea cephalotes* and *lriartea deltoidea* (pers. obs.). Attack can occur during both the pre and post-dispersal phases, and has also been found to be distance- dependent in other tropical rain forests (Wright 1983). These other two palms do not fruit at the sarne season as *Asp-ocaryum.* Post-dispersal predation by bruchids during eady dry season may thus be concentrated heavily on *Astrocaryum* seeds. By the end of the experiments, nearly 100% of the *Astrocaryum* seeds had been killed by predators, a result similar to that of Smythe (1989) for *Astrocaryum standlenyum* in Panama.

Dipteryx seeds are protected by thick endocarp walls and are not attacked by bruchids. They may be attacked prior to germination only by a reduced number of specialist predators such as squirrels, However, when the seeds dry óut, the woody valves crack open making the kernel more vulnerable.

Astrocaryum arid *Dipteryx* seeds may escape predation by being scatterhoarded by rodents such as agoutis. Because agoutis sometimes do not recover buried seeds, some survive and germinate (Smythe 1989, Forget 1990, 1992). For *Astrocaryum standleyanum* in Panama, Smythe (1989) found that after 11 months, 29.2% of buried seeds had germinated, and only 2.6% of those left on the surface survived. ln experiment 2, I found at least 7 *Astrocaryum murumuru* seeds buried by agoutis, which suggests that the sarne patterns could occur at Cocha Cashu.

TIIBEFFECT OF CLUMPING OF ADULT TREES ON SEED SURVIVAL.

Toe survival of *Astrocaryum* seeds placed near adult trees, far from adult trees, and for both treatments combined, was not significantly correlated with the number of trees in adult clumps (Figure 5 a, b and e). On a large spatial scale (50 ha), the lack of a relationship between number of *Astrocaryum* seeds surviving and number of trees in experimental clumps could be due to similar nearest neighbor distances among the trees in each clump. *Astrocaryum* trees were in general much closer to one another than were *Dipteryx* trees. Toe increased clumping of *Astrocaryum* trees may concentrate the activities of predators. Large vertebrate seed-eaters, like the collared peccary *(Tayassu tajacu),* may patrol relatively large areas in search of food. After finding a fruiting tree, they may revisit the tree for severa! days úntil nearly ali seeds are consumed. Then they may extend their search to nearby conspecific trees. This type of distance-dependent seed predation could be important in influencing the spacing between offspring and parent trees in closely spaced groups (see Janzen 1970, Wright 1983, Terborgh et al. 1993).

At a smaller spatial scale (experiment 3 within the 2.5 ha plot), the number of *Astrocaryum* seeds swviving mammalian seed predation was similarly not related to the number of adult trees in clumps. However, there was a significant inverse relationship between *Astrocaryum* seed mortality by insects and the number of trees in a clump, with a lower proportion of seeds being eaten near trees in larger clumps (see Table 3). This indicates that insect seed predators may have been satiated.

Dipteryx seed swvival showed a pattem different from that of *Astrocaryum* . Vertebrate predators seem to favor increased spacing between parent and offspring both under widely separated adult trees (see experiment 1) and within groups of adult tree (as in this experiment). Therefore, natural enemies strongly affected the spatial distribution of potential recruits into the adult population of both tree species.

These patterns of seed predation may help to explain why both widely spaced and clumped adults of both plant species are observed at Cocha Cashu. Wide spacing of adults could be a consequence of low seed and seedling survival near parent trees (the expectation from Janzen-Connel model, Janzen 1970, Connell 1971). Rare clumps of adult trees observed in the area for *Astrocaryum* and *Dipteryx* could result from predator satiation or other factors, such as the occurrence of occasional very large gaps. Satiation of the invertebrate predators of *Astrocaryum* seeds is suggested by the swvival of a higher number of seeds in sites near groups of adult trees than in sites near isolated trees (in the 2.5 ha plot). *Dipteryx* seeds are not attacked by insects. For *Dipteryx,* like *Astrocaryum,* larger numbers of seeds survive near groups of adult trees. Rodents could also cause clumping of adults when they store several to many *Astrocaryum* and/or *Dipteryx* seeds in a small area. Bats also concentrate *Dipteryx* seeds at bat roosts.

Altematively, the observed variation in the spatial relationships of adult trees, from isolated individuals to clumps, could also be due fo constrained regeneration requirements of these two species, which may be met only in occasional places in the forest. Because it is much more abundant, the density of such favorable sites may be higher for *Astrocaryum* than for *Dipteryx*.

Boucher (1981), who studied mammalian seed predation on a tropical lowland oak tree *(Quercus oleiodes),* also suggested that unless adult trees occur in sufficient density, they will fail to satiate predators and consequently fail to regenerate. For *Astrocaryum* at Cocha Cashu, the sufficient density must be high, because seed survival was found to be similar in cluster of adults containing 1-13 trees.

SEED SURVIVAL ANO BEHAVIOR OF SEED PREDATORS

Differences in the results obtained with *Astrocaryum* seed survival in relation to spatial scale (experiments 1, 2 and 3) might reflect the scale of action of two main *Astrocaryum* seed predators, peccaries and spiny rats. White-lipped Peccaries at Cocha Cashu travel in huge herds (> 100 individuals). During foraging, the herds break up so that individuals forage independently over areas of a few hectares (Pers obs.). A herd crossed my 2.5 ha plot twice in two months during the dry season; and each time their behavior was completely different At the time of the first observation, the individuals were widely spaced. But the second time, groups were concentrated on some areas. Scattering of the herd may increase the probability of visiting trees in many different patches.

Toe Spiny rat *Proechmys* spp. is an abundant *Astrocaryum* seed predator in the study area (Janson and Emmons 1991). Toe noctumal movements of this rodent within its small home range of about 0.5 a certainly limits long-distance seed dispersal (Emmons 1982). Because of the small ateas covered by individuals, they may easily detect local variation in seed density. Toe results of Experiment 3 support this possibility. Seed predation by mammals within the 2.5 ha plot was dependent on the size of clumps of adult *Astrocaryum* trees.

An important component of environmental heterogeneity affecting *Astrocaryum* and *Dipteryx* seed seems to be differences in the foraging of the main predators.

Resource concentrations created by piles of seeds around bases of *Astrocaryum* trees is favorable to bruchids. Peccaries usually clean the whole area around an *Astrocaryum* tree in their search for seeds. Terrestrial rodents do the sarne, but in the course of repeated visits. Bruchids are more resident in this microenvironment than the other two main predators because they depend on *Astrocaryum* seeds to complete their life cycles. Toe combined impact of the two classes of predators on *Astrocaryum* seeds around an adult tree is very high.

DENSITY AND DISTANCE EFFECTS ON SEEDLING SURVNAL

The survival and spacing patterns of *Astrocaryum* seedlings I observed at Cocha Cashu support the escape hypothesis (Howe and Smallwood 1982) and the predictions of Janzen-Connell model. ln 1992, seedling longevity was dependent on the proximity of adult trees. *Astrocaryum* seedling survival far from adult trees was higher than beneath them, indicating escape in distance (Table 5). Early distance-dependent mortality caused *Astrocaryum* seedlings to be less clumped around adults than they would have been had seedlings died uniformly everywhere. Distance to nearest neighbor and seedling density had no significant effects on *Astrocaryum* seedling survival (Table 5).

ln 1993, *Astrocaryum* seedling survival did not show any detectable spatial patterns. Distance and density relationships were probably obscured by the effects of environmental heterogeneity created by a wave of recruitment of new seedlings within the plot after 1991. A contrasting result was found by Vandermeer (1977) in Costa Rica, who found an inverse distance-dependent survival for seedlings of the palm, *Welfia georgii.* He found higher seedling survival within 3 m of adults than at > 3 m from adults. However, his analysis was static, because he did not consider more than one year in seedling survival. Differences among years in the pattems of seedling survival indicate differences in the corresponding population recruitment curves. Augspurger (1983) found population recruitment curves peaking at different distances in different years for various tropical trees in Panama.

Dipteryx seedling survival pattems were the reverse of those found for *Astrocaryum* seedlings, and did not support the escape hypothesis. ln 1992, *Dipteryx.* showed no significant differences in the proportion of seedlings surviving near and far from adult trees. However, in 1993 *Dipteryx* seedling survival was inversely related to distance from parent trees (i.e more seedlings survived close than further from parent (Table 6).

These results contradict those found in Costa Rica for *Dipteryx panamensis* seedlings (Clark and Clark 1984). Perhaps these differences between Cocha Cashu and Costa Rica in the pattems of *Dipteryx* seedling survival are due to differences in the height of *Dipteryx* trees at the two locations. *Dipteryx* adults are much taller at Cocha Cashu, thereby possibly preventing other trees, which shade plants in the lower understory, from growing beneath them. Therefore, adults may improve the light environment for *Dipteryx* seedlings. However, if true, such a positive influence is ephemeral, because almost all seedlings beneath adults die within a few years, due mainly to predation. Eventual mortality of seedlings is indicated by the almost complete absence of saplings beneath the majority of adults in my study area (see also Clark and Clark 1984, 1987).

Contrasting tendencies in the distance dependence of population recruitment in *Astrocaryum* and *Dipteryx* could explain why adult *Astrocaryum* trees are more uniformly distributed (expectation from Janzen's model) and *Dipteryx* trees are clumped (expectation from Hubbell's model) (in some sites) at Cocha Cashu. Real recruitment of *Dipteryx* beneath adults is rare. Only two saplings 2 m height were found in the 2.5 ha plot. Both tree species show high variance in crop size, seed and seedling predation rates, and temporal variation in seedling survivorship, which could reduce the strength of spacing patterns predicted by the Janzen-Connell model. Therefore, studies which employed severa! adults and followed seedling performance for more than one year would decrease the risk of incorrectly generalizing the results obtained (Augspurger 1983, Oark and Clark 1994).

RECRUITMENT OF *Astrocaryum* and *Dipteryx* AND DIVERSITY IN THE 1ROPICS

In the initial phase of recruitment of *Astrocaryum* and *Dipteryx* the two plant species at Cocha Cashu showed two contrary patterns. For *Astrocaryum* , the post-dispersal seed phase seems more criticai than the seedling phase. Seed mortality is higher than seedling mortality, with a low escape in space. In this study, this pattern is valid only for mammal predation. However, seed dispersai to some distance from adult trees may be advantageous for *Astrocaryum* in enhancing escape from bruchid beetles (Terborgh et al. 1993). *Astrocaryum* seedlings may also escape predation by mammals if established at some distance from the parent tree. But escape could be dependent also on previous population recruitment as this study suggests. In the *Astrocaryum* population within the 2.5 ha plot, the distances in each of the population recruitment curve peaks may vary, but this peak of recruitment may not occur very far from the adult trees.

Evidence of this is the presence of *Astrocaryum* plants of different age classes segregated at different distances producing concentric rings around adult trees.

Toe pattems of *Dipteryx* survival also differs from seeds to seedlings. Predation resulted in a higher impact on seeds than on seedlings. Establishment out to 40 m from the adult trees will not be advantageous for *Dipteryx* seedlings because he probability of survival is lower than beneath the parent trees (Table 6), at least for the first two years after establishment. *Dipteryx* as well as *Astrocaryum* seedling survival will vary in years of high and low recruitment. Larger numbers of seedlings surviving under parent trees in 1993 may have been a consequence of the 1992 "masting year, " which might have satiated predators.

An important density-independent factor affecting seedling survival is branch fall. *Dipteryx* trees develop large branches, which commonly break off due to large size and weight. It is common to find gaps and limbs beneath *Dipteryx* trees, which were created by their own branch falls. At Cocha Cashu, rodents such as agoutis store seeds near logs. They may do this to wait for the seeds to dry and germinate, because t ey are easier to open then. Also by hiding seeds terrestrial rodents may avoid competition with the mainly arboreal squirrels, which are *Dipteryx* seed specialists. Decreased insect predation on *Dipteryx* seeds scatterhoarded near logs may enhance the production of seedlings near the parent trees.

Toe actual abundance of *Dipteryx* and *Astrocaryum* at Cocha Cashu may result from a balance of two different population responses to the biological environment: 1) high establishment during years of high seed production when predators are satiated; 2) poor dispersa! in years of low seed production resulting in few seedlings.

Another important conclusion of this study is that distance-dependent survival of *Astrocaryum andDipteryx* seeds and seedlings are dependent on spatial scale. The results for both plant species support Schupp's idea that the results of processes at the leve! of an individual tree are not necessarily representative of processes at the population level (Schupp 1992). Toe Janzen-Connell model predicts that local tree diversity would be maintained when both density and distance dependent processes are affecting progeny survival. However, the proportion of trees of a given species showing this pattern within a population or community, and also the frequency with which it occurs over the long run would also be important to determining local diversity. Which then of the two models is the most correct, the Janzen-Connell or Hubbell?. It depends on the spatial scale in which the study is conducted. Also density/distance dependent mortality can be a function of the plant species, year, and types of predators and their different types of foraging behavior.

Allelopathic secretions which can inhibit the growth both of other species' seedlings or the seedlings of the producing tree could generate a greater than expected level of spacing. In Australia, the forest tree *Grevi/lea robusta* prevents the establishment of saplings in its vicinity by secreting a toxin from its roots (Webb et al. 1967). Competition for nutrients between parent trees and offspring could produce similar effects.

Density-independent seed and seedling mortality produced by abiotic factors such as variation in amount of light, leaf litter and understory vegetation cover, litterfall, presence of forest objects, and tree-fall gaps, have also been suggested to play an important role in this system (see chapters 1, 3, and 4). Because such factors can potentially create environmental heterogeneity, they may obscure density/distance-dependent mortality patterns (see chapters 1, 2 and 3 of this study, and also Kiltie 1981, Augspurger 1984, Clark and Clark 1984, 1987, Molofsky and Augspurger 1990, Denslow et al. 1991, Augspurger and Kitajima 1992).

Finally, two general conclusions can be drawn from this study: 1) the pre-gennination phase seems to be the most critical period in the population recruitment of these two plant species because this is when most mortality occurs; 2)the action of predators on *Astrocaryum* and *Dipteryx* seeds and seedlings may help to maintain local tree diversity because it prevents adult trees from monopolizing the space around them with their progeny, thereby creating opportunity for other plant species to establish.

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Table 1 . Survival of ***Astrocaryum* and *Dipteryx*** seeds under three distance treatments and three seed densities treatments (Cox Proportional Hazard Regression). See text for further details.

Parameter	DF	Estimate(SE)	z	Sig. level
Astrocaryum +				
Target tree	10	0.034 (0.006)	5.42	***
Distance	3	-0.031 (0.022)	-1.45	ns
Seed density	3	0.009 (0.003)	2.60	**
Dipteryx++				
Target tree	10	-0.141 (0.020)	-7.26	***
Distance	3	-0.063 (0.031)	-2.03	*
Seed density	3	1.002 (0.005)	0.36	ns

***, p<0.0001; **,p<0.001; *, p<0.05; ns, not significant.
+Likelihood ratio test=38.3 on 3 DF, p<0.000001; ++ Likelihood ratio test=56.9 on 3 DF, p<0.000001

Table 2. Results of three-level factorial Analysis of Variance (ANOVA) on time at 50% seed survival (weeks), of *Astrocaryum* and *Dipteryx* seeds in: target trees (first levei, ten *Astrocaryum* and five *Dipteryx* trees); distance from a target tree (second levei, three distances treatments, seeds on the litter near the trunk of the target tree, seeds on the litter under the crown edge, seeds on the litter far from the target tree); and seed number (third levei, seed number of four, eight, and sixteen seeds placed in 30 x 30 cm plots). See text for further information.

Source of variation	SS	DF	M S .	F
Astrocaryum				
Tree	64.831	9	7.203	20.94***
Distance	0.206	2	0.103	0.30ns
Seednumber	0.138	2	0.069	0.20ns
Tree*distance	6.048	18	0.336	0.98ns
Tree*seed number	5.553	18	0.308	0.90n
Distance*seed number	2.016	4	0.504	1.47ns
Tree*distance*seed number	6.333	36	0.176	0.51ns
Error	92.869	270	0.349	
Corrected total	177.996	359		
Dipteryx				
Tree	11.861	4	2.965	15.68***
Distance	0.118	2	0.059	0.31ns
Seednumber	0.149	2	0.075	0.40ns
Tree*distance	1.578	8	0.197	1.04ns
Tree*seed number	1.632	8	0.203	1.08ns
Distance*seed number	0.488	4	0.122	0.64ns
Tree*distance*seed number	1.852	16	1.852	0.6lns
Error	25.852	135	0.189	
Corrected total	43.216	179		

+ For both *Astrocaryum* and *Dipteryx*, the response variable, time at 50% seed survival was root-squared transfonned to approximate normal distribution. *** p=0.0001; ns=not significant.

Table 3. Results of Multiple Regression Analysis of the of response variable mean proportion of *Astrocaryum* seeds preyed upon by insects, on the independent variables: seed density and size of the clumps of adult trees in a given forest patch within the 2.5 ha plot.

Overall Regression $r^2 = 0.812$ n= 10

	SQ	MS	DF	F	p
Regression	0.106	0.053	2	15.150	0.003
Residual	0.025	0.004	7		

Partial Regression (contributions from independent variables)

	Coef.	t-value	p
Constant	0.837	20.330	0.000
Seed density	-0.012	-4.734	0.002
Size of adult tree group	-0.014	0.004	0.016

Table 4. Results of Multiple Regression Analysis of the of response variable mean proportion of *Astrocaryum* seeds preyed upon by mammals, on the independent variables: seed density and size of the groups of adult trees in a given forest patch within the 2.5 ha plot.

Overall Regression $r^2 = 0.676$ n = 10

	SQ	MS	DF	F	p
Regression	0.030	0.015	2	7.300	0.019
Residual	0.014	0.002	7		

Partia! Regression (contributions from independent- variables)

	Coef.	t-value	p
Constant	-0.037	-1.186	0.274
Seed density	0.007	3.506	0.010
Size of adult tree group	0.006	1.789	0.117

+ the response variable was arc-sine transformed to approximate normal distribution

Table 5. Results of Logistic Regression Analysis of response variables *Astrocaryum* seedling survival in 1992 and 1993, on independent variables: seedling distance to the nearest neighbor, seedling density (number within 5 m radius around each seedling), distance to the closest adult tree and density of adult trees (number within 20 m radius around each tree).

Astrocaryum 1992, (N=538)

Variable	Parameter Estimate	Standard Error	Wald $x2$	Standardized Estimate	p-value $x2$
Intercept	1.7127	0.730	5.504	...	0.0190
Dist. seedling	-0.1115	0.174	0.409	-0.0648	ns
Seedl. density	0.0146	0.019	0.595	0.0844	ns
Dist. adult tree	0.1016	0.049	4.223	0.2169	*
Tree density	0.0426	0.107	0.159	0.0368	ns

Astrocaryum 1993, (N=479)

Variable	Parameter Estimate	Standard Error	Wald $x2$	Standardized Estimate	p-value $x2$
Intercept	2.2526	0.599	14.131	...	0.0002
Dist seedling	-0.1510	0.129	1.356	-0.0853	ns
Seedl. density	-0.0226	0.014	2.630	-0.1226	ns
Dist. adult tree	-0.0189	0.036	0.282	-0.0385	ns
Tree density	-0.0256	0.081	0.098	-0.0214	ns

* $p < 0.05$; ns= not significant, $p > 0.10$

Table 6. Results of Logistic Regression Analysis of response variables *Dipteryx* seedling survival in 1992 and 1993 on independent variables: seedling distance to the nearest neighbor, seedling density (number within 5 m radius around each seedling), distance to the closest adult tree and density of adult trees (number within 20 m radius around each tree).

Variable	Parameter Estimate	Standard Error	Wald XZ	Standardized Estimate	p-value XZ
Dipteryx 1992, (N=169)					
h)tercept	0.080	0.507	0.025	...	0.8034
Dist. seedling.	-0.1026	0.082	1.566	-0.1702	ns
Seedl. density	0.010	0.011	0.945	0.0956	ns
Dist. adult tree	0.0123	0.035	0.120	0.0453	ns
Dipteryx 1993, (N=105)					
Intercept	1.8456	0.739	6.224	...	0.0126
Dist. seedling.	-0.0139	0.056	0.061	-0.049	ns
Seedl. den_sity	-0.0017	0.021	0.007	-0.011	ns
Dist. adult tree	-0.1055	0.049	4.575	-0.357	*

* p< 0.05; ns= not significant, p>0.10

Figurel. Field experimental design used to test the escape hypothesis for ***Astrocaryum*** and ***Dipteryx*** seeds. Each square is a 30 x 30 cm plot, located under four replicates of each seed density (numbers within the squares) and at three different distances from the experimental trees (O m, **5** m and 20 m for ***Astrocaryum*** and Om, 10 m and 40 m for ***Dipteryx).*** See methods for further details.

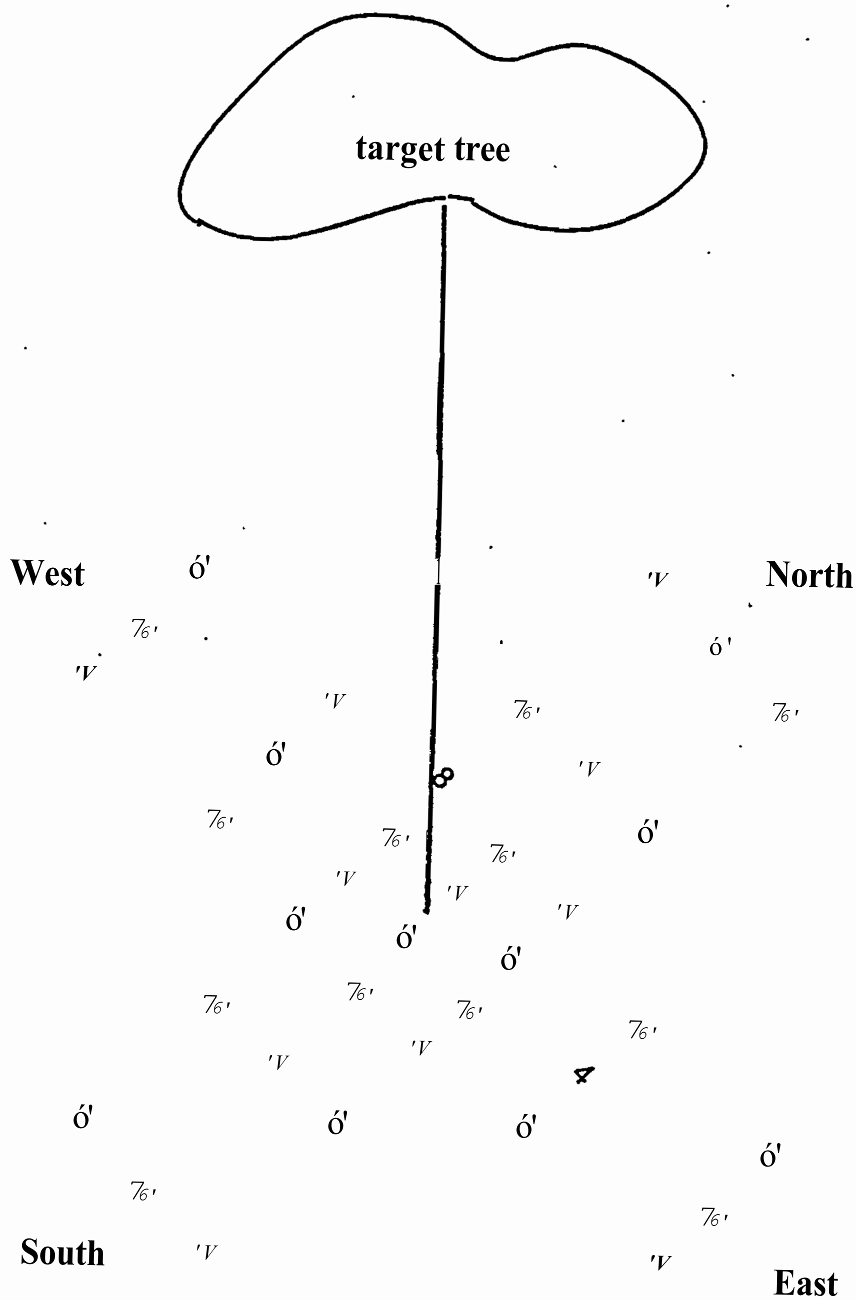
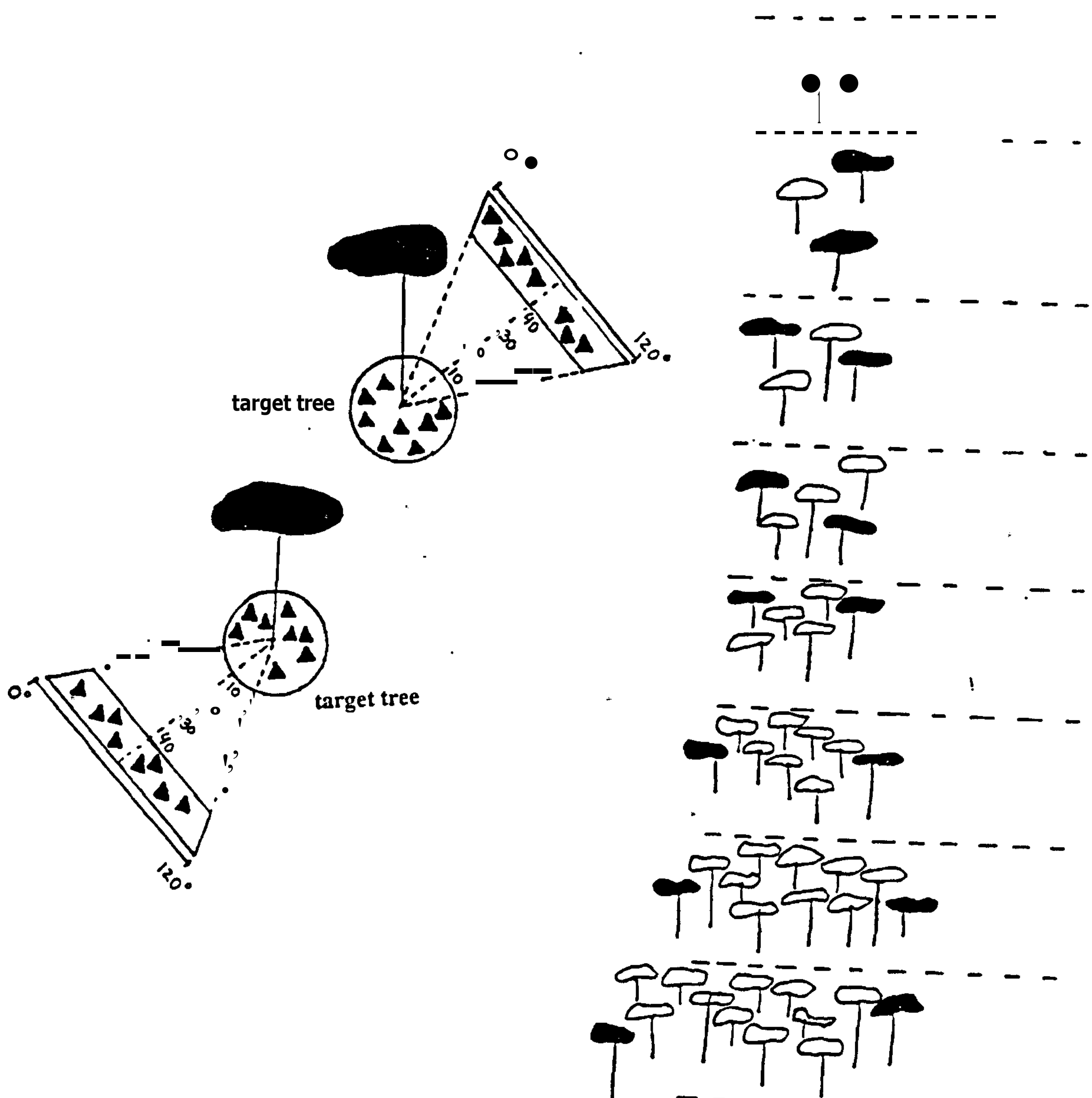
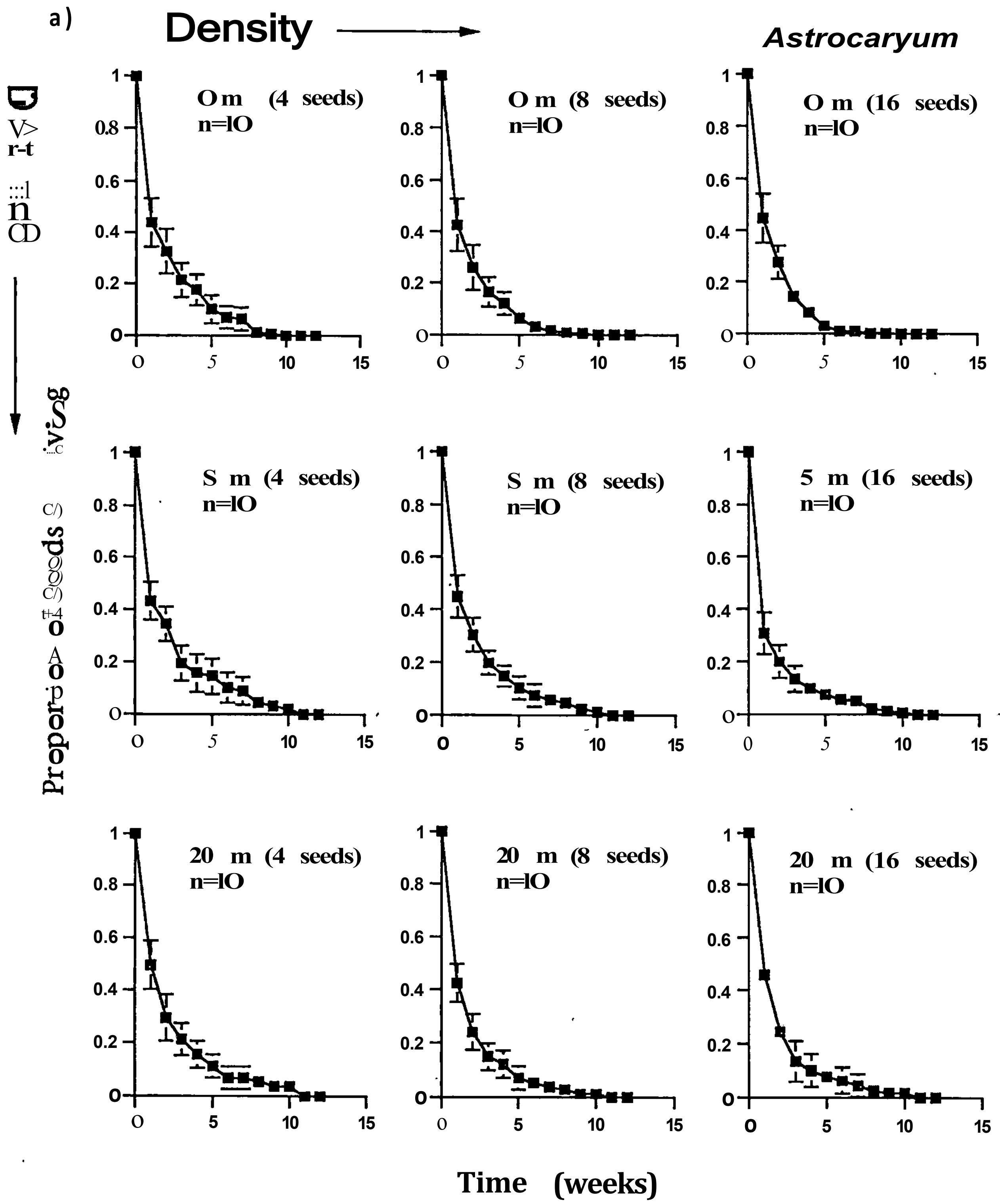

target tree
West
North
8
4
South
East

Figure 2. Field experimental design· for experiment 2. In this experiment seeds were placed both on the ground beneath adult trees and farther from the adult trees. Adult trees wer located in groups bearing different numbers of trees of that species. This design w used for *Astrocaryum andDipteryx* seeds. See methods for further details.



size of the groups of adult trees used

Figure 3- a. Descriptive survival curves for *Astrocaryum* seeds under three seed densities (4, 8 and 16 seeds) and under three experimental treatments: seeds placed on the ground beneath the target tree (O m), seeds placed on the ground at tree crown edge or 5 m from the target tree trunk; and seeds placed at 20 m from the target tree; b. Survival curves for *Dipteryx* seeds under the sarne three densities (4, 8 and 16 seeds) and under three experimental treatments: seed placed on the ground beneath the target tree (O m), seeds placed on the ground at tree crow edge (10 m from the trunk) and seeds placed on the ground 40 m from target trees. There were four replicates per seed density in each treatment for each one of the 10 *Astrocaryum* adult trees and 5 *Dipteryx* adult trees used (see experimental design Figure 1).The squares along the curves are means and the vertical bars are standard error values.


a)
Density
Astrocaryum
0 m (4 seeds)
n=10
0 m (8 seeds)
n=10
0 m (16 seeds)
n=10
5 m (4 seeds)
n=10
5 m (8 seeds)
n=10
5 m (16 seeds)
n=10
20 m (4 seeds)
n=10
20 m (8 seeds)
n=10
20 m (16 seeds)
n=10
Time (weeks)

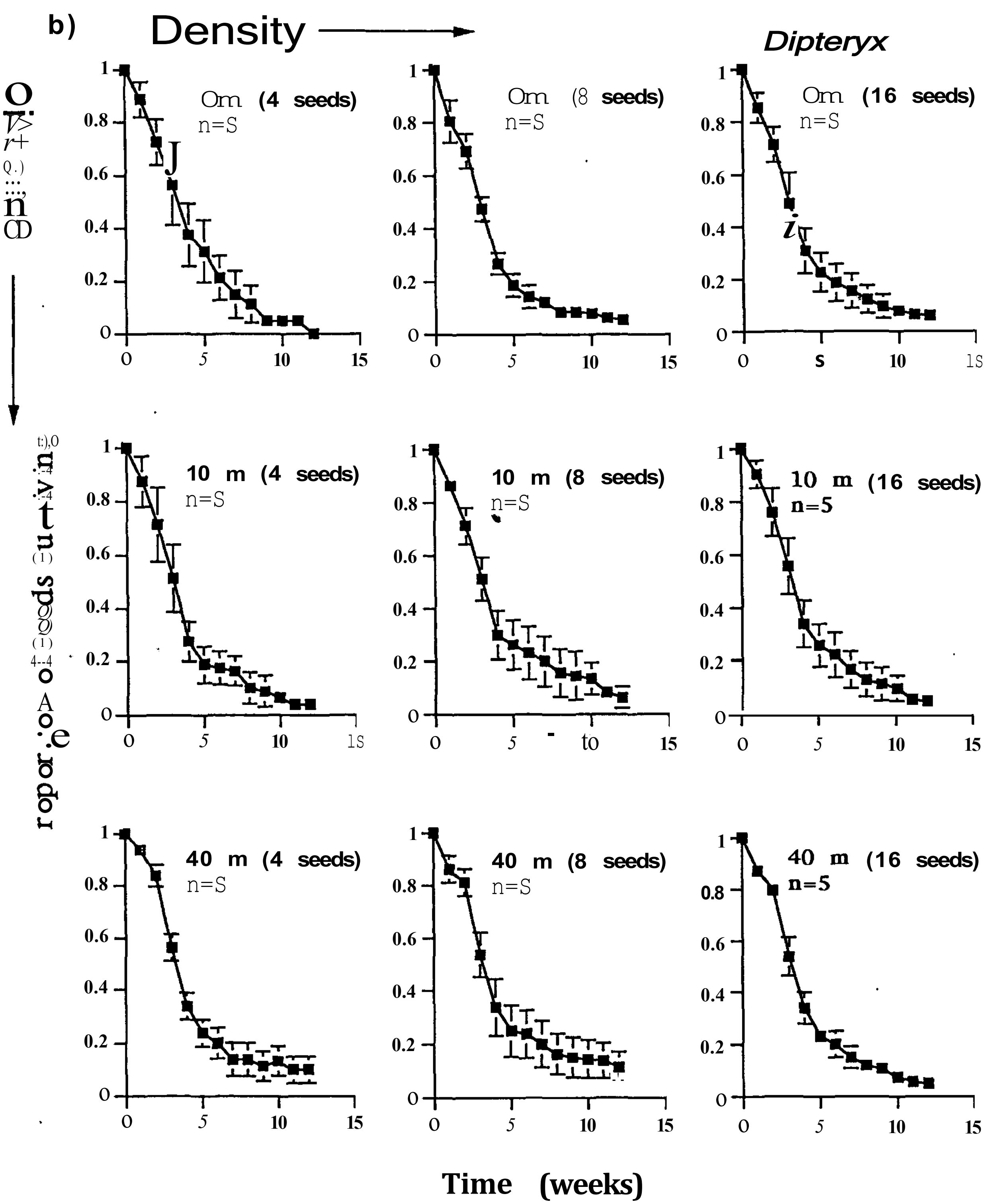
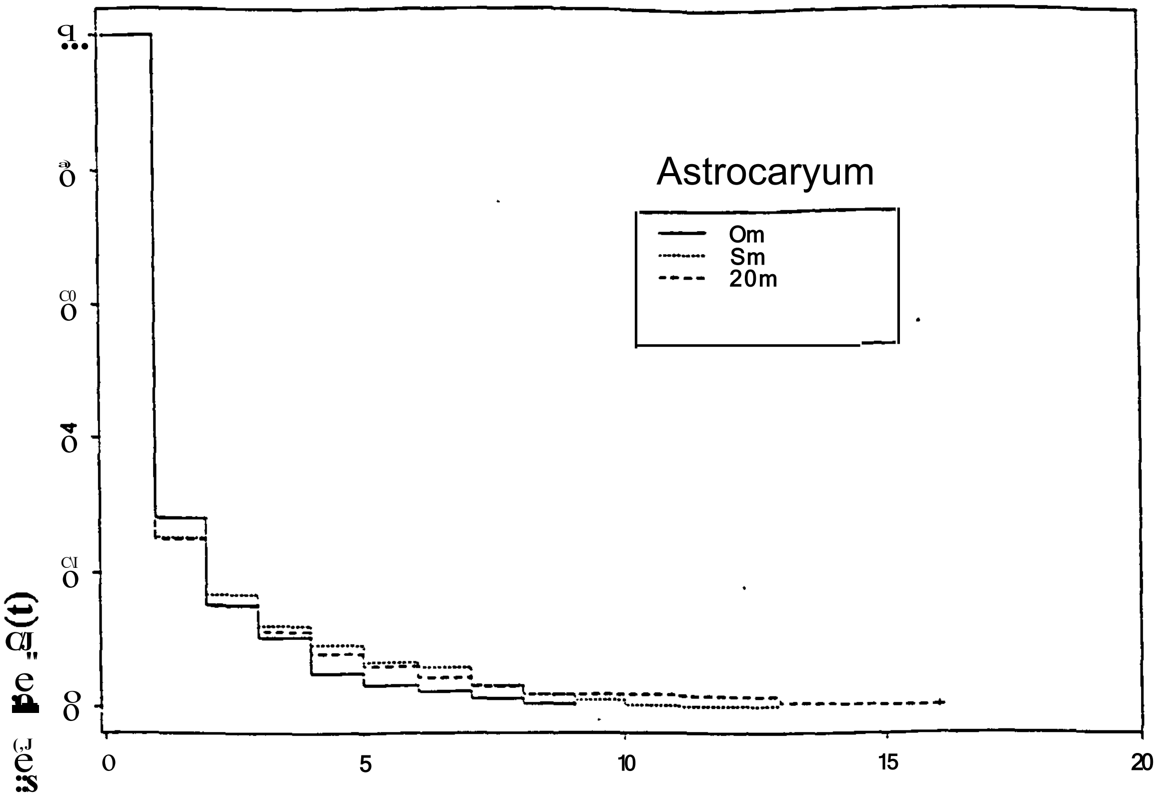

b)
Density
Dipteryx
0 m (4 seeds)
n=5
0 m (8 seeds)
n=5
0 m (16 seeds)
n=5
10 m (4 seeds)
n=5
10 m (8 seeds)
n=5
10 m (16 seeds)
n=5
40 m (4 seeds)
n=5
40 m (8 seeds)
n=5
40 m (16 seeds)
n=5
Time (weeks)

Figure 4. Survival functions for seeds in experiment 1, in which I investigated *Astrocaryum* seed survival in relation to distance from focal trees and seed number. Toe ordinate represents the proportion of the initial population of seeds that was still alive at the start of each weekly census interval. The upper graphs present the seed survival curves for the different "distance treatments" in which experimental seeds were placed at Om, 5 m, and 10 m for *Astrocaryum.* focal trees; Toe lower graphs are for seed number treatment.

Astrocaryum seed survival was not significantly different between the three " distance treatments" (upper graph). *Astrocaryum* seed survival did not differ with seed number (lower graph). Initial .seed survival of *Astrocaryum* seeds was significant between distance treatments ("Wilcoxon test", $x2$ = 10.2, DF = 2, p = 0.006). Differences between distances treatments in late seed survival were not significant ("Log Rank test", X^2 = 3.7, DF = 2, p = 0.157). Seed number treatments showed significant differences in early seed survival ("Wilcoxon test", $x2$ = 6.4, DF = 2, p = 0.0003). Differences between seed number on late seed survival were also significant ("Log Rank test", $x2$ = 11.2, DF = 2, p = 0.004).


Astrocaryum
Om
Sm
20m
0
5
10
15
20

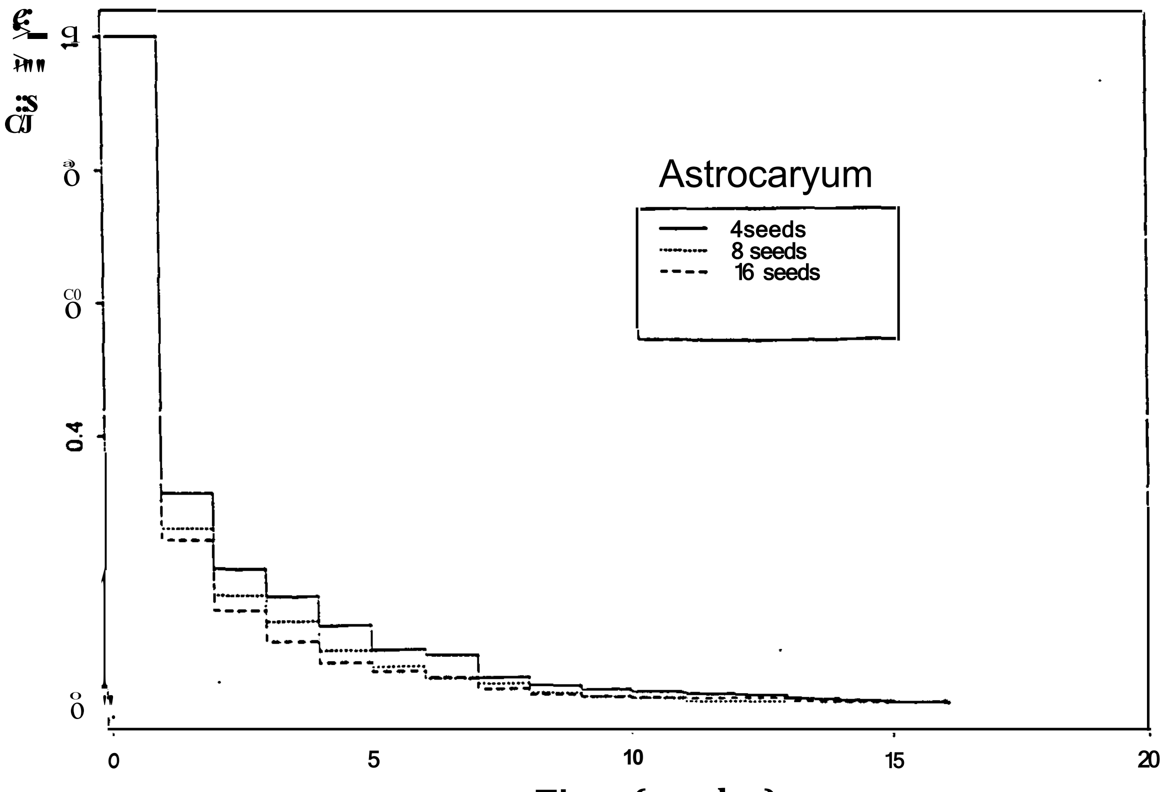

Astrocaryum
4seeds
8 seeds
16 seeds
0.4
0
5
10
15
20
Time (weeks)

Figure 5. Survival functions for seeds in experiment 1, in which I investigated ***Dipteryx*** seed survival in relation to distance from focal trees and seed number. The ordinate represents the proportion of the initial population of seeds that was still alive at the start of each weekly census interval. The upper graphs present the seed survival curves for the different "distance treatment" in which experimental seeds were placed at Om, 10 m, and 40 m for ***Dipteryx*** focal trees. The lower gráphs are for seed number treatment.

Dipteryx seed survival was significantly different between the three " distance treatments" (upper graph). ***Dipteryx*** seed survival did not differ with seed number (lower graph). Initial seed survival of ***Dipteryx*** seeds was not significant between distance treatments ("Wilcoxon test", $X2 = 3.4$, DF = 2, p = 0.110). Differences between distances treatments in late seed survival was significant Ç'Log Rank test", x2 =5.1, DF = 2, p = 0.052). Seed number treatments showed no significant differences in early seed survival ("Wilcoxon test", x2 =0.4, DF = 2, p .823). Differences between seed number on late seed survival were also not significant ("Log Rank test", x2 =0.4, DF =2, p = 0.809).

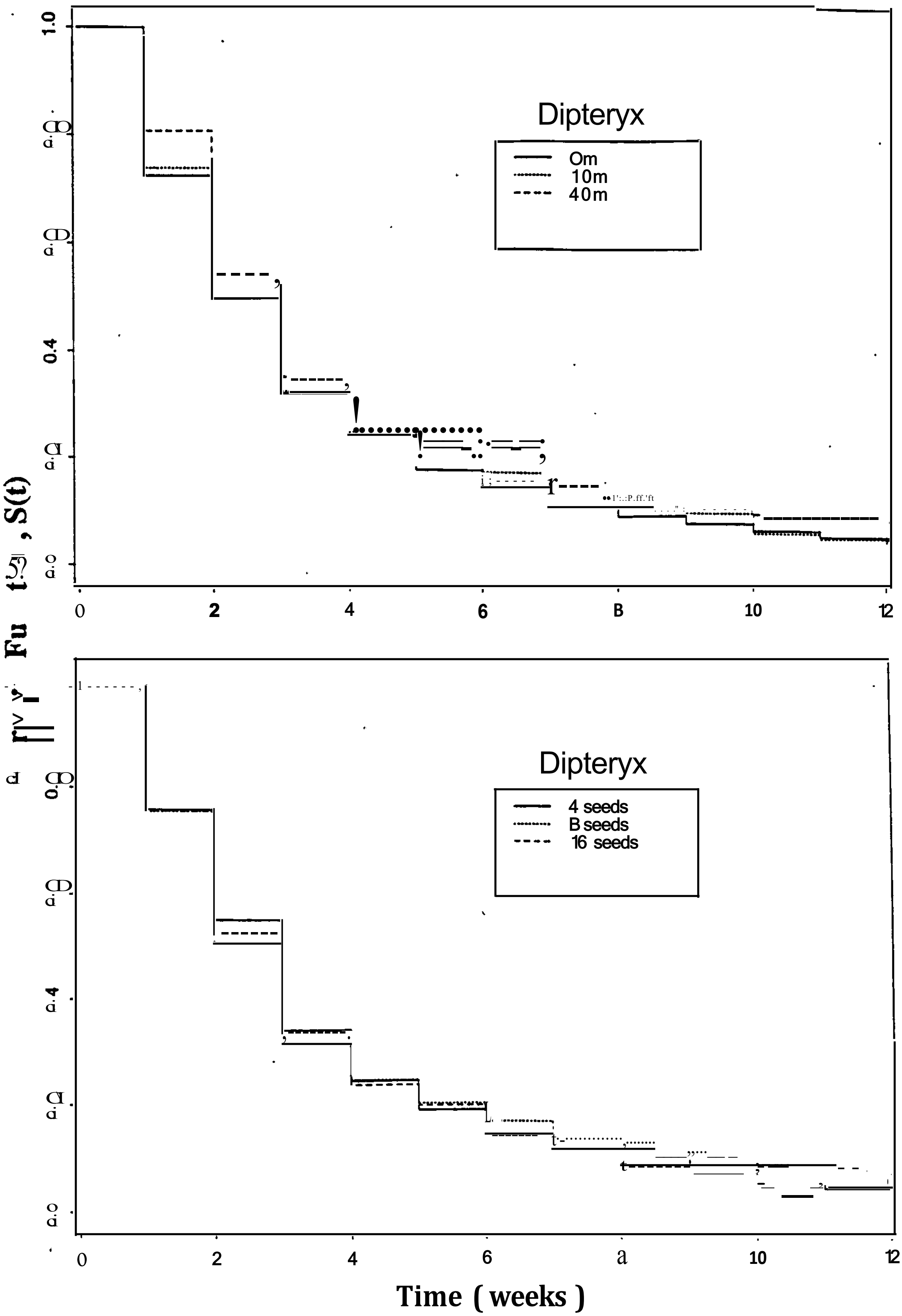

Dipteryx
Om
10m
40m
Dipteryx
4 seeds
B seeds
16 seeds
Time (weeks)

Figure 6.- (a) Number of seeds surviving beneath an adult *Astrocaryum murumuru;* (b) number of seeds ative 20 m away from the adultA.. *murumuru,* and (e), total number of *Astrocaryum* seeds surviving (beneath plus away) as functions of the number of adult trees present in a given patch of forest surrounding the two target trees used to place the experimental seeds. Graphs (d), (e) and (f) are the sarne relationships as graphs (a), (b) and (e) but for *Dipteryx micrantha* trees and seeds. It was not necessary to perform transformations in any of the dependent variables used for these analyses. The only si cant íegression was for (e), which equation and coeficient are given in the figure.

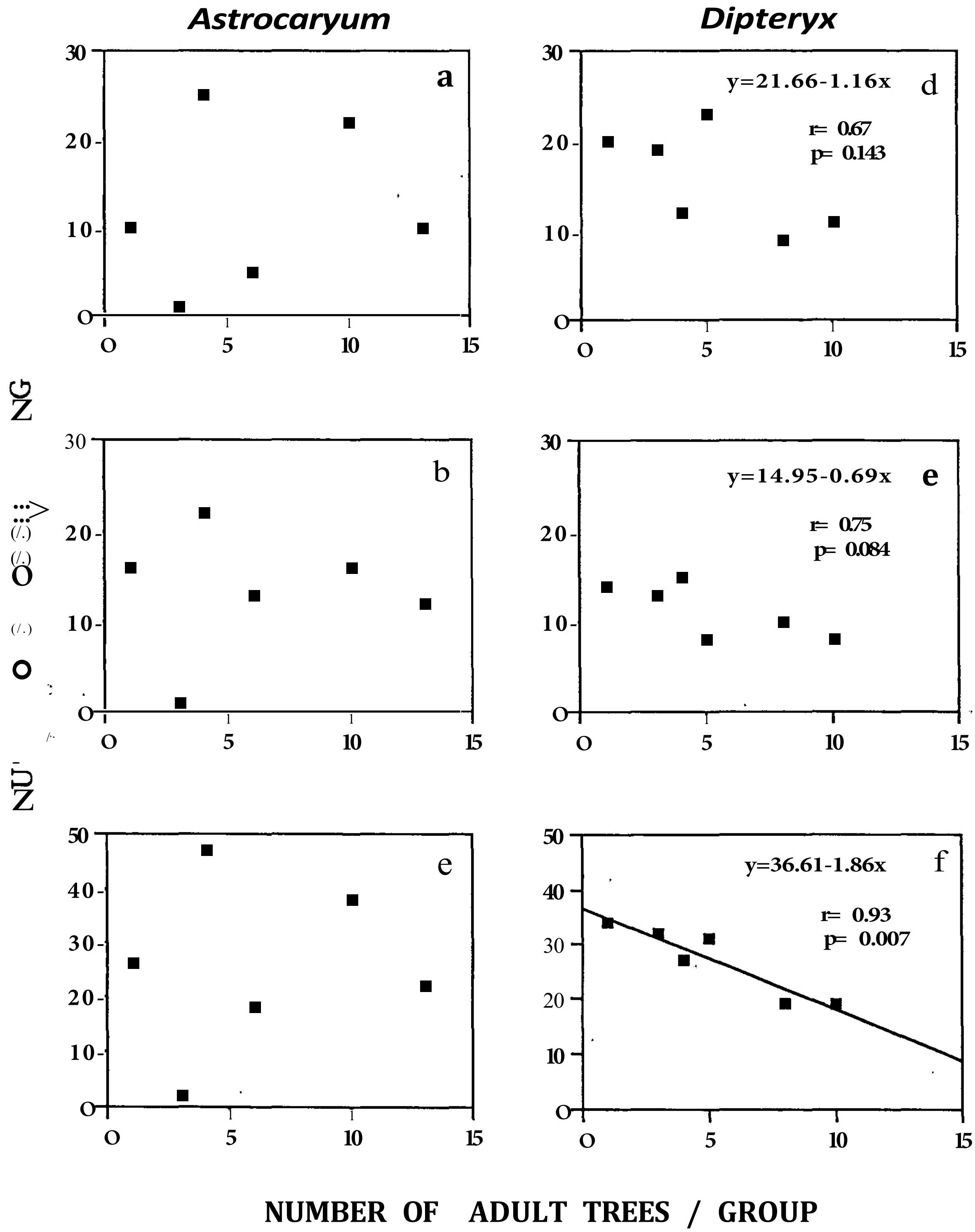
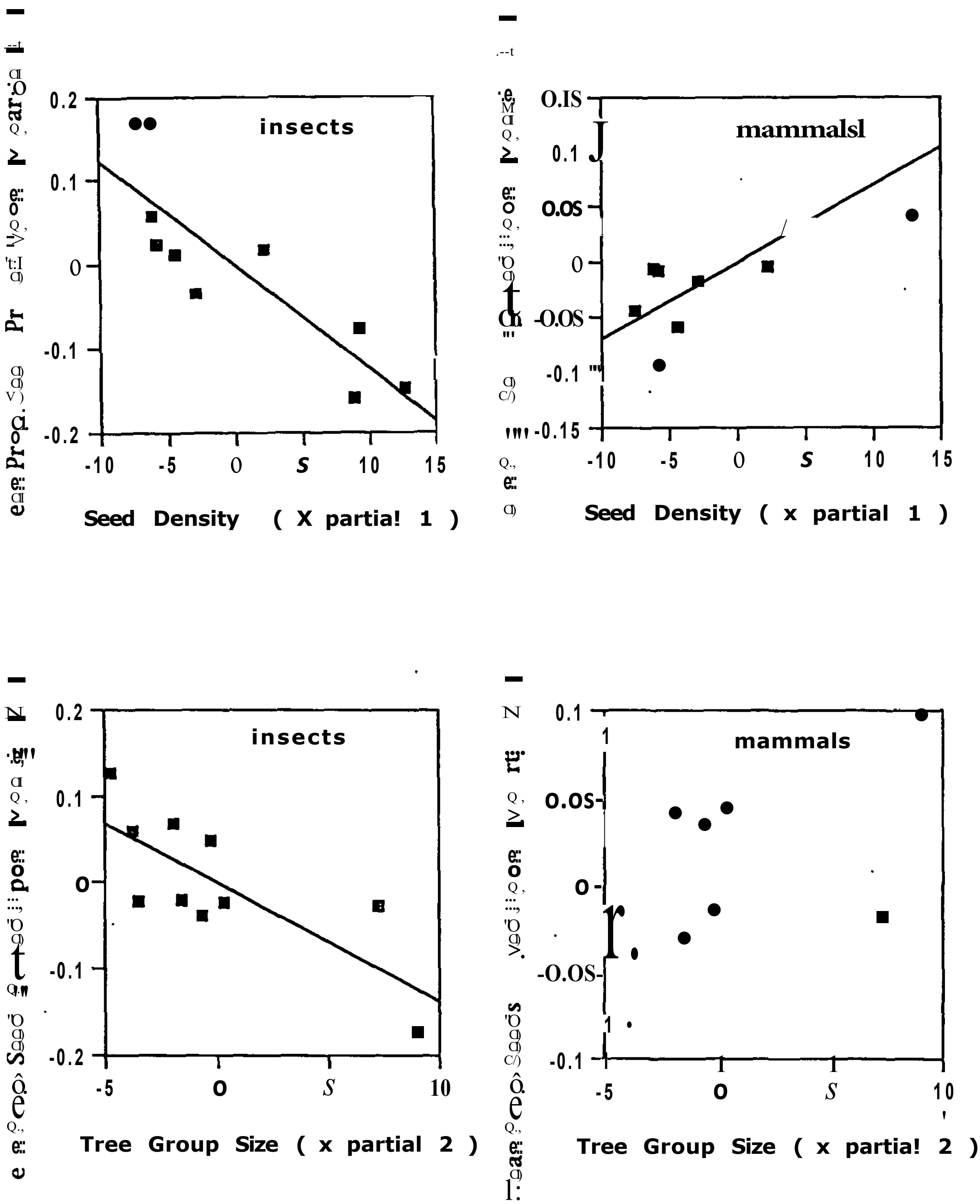

Astrocaryum
Dipteryx
a
b
e
y=21.66-1.16x
d
r= 0.67
p= 0.143
y=14.95-0.69x
e
r= 0.75
p= 0.084
y=36.61-1.86x
f
r= 0.93
p= 0.007
NUMBER OF ADULT TREES / GROUP

Figure 7. Parti.al regression plots of the residuals of the response variable mean proportion of *Astrocaryum* seeds preyed upon by insects (graphs on left) and by mammals (graphs on right) against the residuals of each one of the independent variables *Astrocaryum* seed density and number of adult trees/clutch of trees in a given patch of forest. Both variables (response and independent) were regressed on the other two independent variables of the model. (residuals for each of the four plots come from the multiple regression analysis of Tables 3 and 4).


insects
Seed Density (X partial 1)
mammals
Seed Density (x partial 1)
insects
Tree Group Size (x partial 2)
mammals
Tree Group Size (x partial 2)

Chapter4

SEED AND SEEDLING SURVIVAL OF *Astrocaryum murumuru* (Mart.) AND *Dipteryx micrantha* IN GAPS IN TIIE AMAZON FOREST: TESTING TIIE COLONIZATION HYPOTIIESIS.

Summary

Recently, the role of" regeneration strategies" in structuring tropical tree communities has been a focus of attention of tropical ecologists. Canopy discontinuities created by tree-falls are considered to be critical _to many rain forest trees for establishing and completing their life cycles. In this chapter I investigate whether it is advantageous for two common large-seeded and shade-tolerant Amazonian tree species to have their seeds dispersed to gaps. I also explore the role of gaps in promoting the post-germination establishment of seedlings. Toe experiments test the colonization hypothesis which assumes that seed dispersa! augments the probability that some propagules will reach a gap or favorable site where the probability of seedling establishment and survival is higher (Howe and Smallwood 1982).

I simulated the dispersa! process by placing experimental seeds and seedlings in gaps and in the continuously shady understory, and then following their performance. I used seeds and seedlings from two tree species, the palm *Astrocaryum murumuru* , and the legume, *Dipteryx micrantha.* I used standard statistics and Cox Proprortional Hazard models to estimate the survival functions and compare survivorship curves of experimental seeds. Survival of *Astrocaryum* seeds and of *Dipteryx* seeds and seedlings

were higher in two gap zones (crown and bole) than in the shady understory (both near and far away from an adult conspecific). By the end of the experiment, when very few seeds remained, a higher number had survived within gaps. A higher number of seedlings of both plant species also smvived within gaps than in the shady understory over an 18-week period. Even one year after the seedlings had beeen transplanted into gaps, these patterns held. I also found that naturally occurring *Astrocaryum* seeds survived better beneath trees located near gaps than beneath trees located farther away. Variation in gap size was significant for *Dipteryx* seeds, but not for *Dipteryx* seedlings and *Astrocaryum* seeds and seedlings. *Dipteryx* seeds survived longer in small than in large gaps. This study confirms predictions of the colonization hypothesis. Overall the results suggest that, by colonizing tree-fall gaps, these two plant species may improve their chances to complete their life cycles.

Introduction

Seed dispersa! is a crucial phase in the life history of tropical trees. It is during the pre-germination and seedling establishment stages when most mortality occurs (Janzen 1970, Harper 1977, Howe and Smallwood 1982, Louda 1989). High mortality at early stages limits the number of recruits a plant population can produce (Augspurger 1984). Seed dispersa! and survival are also important to understanding the processes of regeneration and the mechanisms that perpetuate divers_ity (see Janzen 1970, Van der Pijl 1972, Mckey 1975, Hartshom 1978, Hubbell 1979, Clark 1986, Fenner 1985, Estrada and Flemming 1986, Whitmore 1989, Garwood 1989). However, empirical investigations of the advahtages of seed dispersa! in tropical regions are available for only a few plant species and areas (Clark and Clark 1984, Howe et al. 1985, Schupp 1989, Howe 1991, Porget 1993, Terborgh et al. 1993).

Tropical trees differ in their requirements for regeneration. Species have been classified as gap colonizers or understory recruiters (Swaine and Whitmore 1988), oras falling on a continuous spectrum of regeneration niches (Grubb 1977, Denslow 1987, Lieberman et.al. 1989).

It has been estimated at about 75% of tropical tree species require a 'light gap phase' in their life cycles in order to attain maturity (Hartshom 1978). Light gradients within gaps may accommodate a range of recruitment niches, in which the extremes are umbrophilia and heliophilia (Grubb 1977, Denslow 1980, Brokaw 1987). Requirements for seed dispersa! and seed survival are also important in determining the ability of a given plant to establish and reach maturity in any particular site.

It is therefore important to know whether coexisting tropical tree species differ in their responses to a given environmental factor such as tree-fall gaps (Lieberman et al. 1989). Some recent studies analyzing seed size distribution in relation to gaps (Poster and Janson 1985), species responses to gap availability (Murray 1986), and presence and quantity of leaf litter (Molovsky and Augspurger 1992), indicate that tree species occupy a range of regeneration niches (Grubb 1977, Denslow 1987, Brandani et. al. 1988).

Gap dynamics and their relevance to tree regeneration are important to understanding tropical diversity. Gaps have therefore been the focus of many publications (Whitmore 1984, 1989, Clark 1986, Clark 1991, Bazzaz 1984, Hubbell and Poster 1986, 1990, Uhl et al. 1988, Alvarez-Buylla and García-Barrios 1992). Recently, many types of plant associations have been re-analyzed with i:espect to disturbance and habitat heterogeneity (Platt and Strong 1989).

In this study, I investigated the consequences of seed dispersa! to tree-fall gaps vs shady understory for two common Amazonian tree species. I tested the colonization hypothesis, which is related to Orians (1982) model of gap dynamics and the escape hypothesis (Howe and Smallwood 1982). Toe escape hypothesis was first envisioned by Ridgley (1930), and later modeled by Janzen (1970) and Connell (1971).

Toe colonization hypothesis postulates that seed dispersai augments the probability that some propagules will fali in a gap or other site where the probability of seedling slllVival and recruitment is greater than random points in the forest. Similarly, the escape hypothesis proposes that mortality is lower at sites removed from the parent tree than near the parent tree. Seed dispersai should increase the probability that propagules colonize a gap. Seeds would then escape from the negative effects of high mortality produced by predators in the vicinities of parent trees (Janzen 1970, Connell 1971, Howe and Smallwood 1982).

The colonization hypothesis is not fully independent of the escape hypothesis, or the parental effects on seed and seedling survival due to negative distance and density effects (Janzen 1970, Howe and Smallwood 1982, Schupp 1988). This is because fruiting trees may be located inside, at the periphery, and away from gaps. Therefore, parental effects should be tested as complementary treatments in the sarne experiment. To my knowledge, only two studies have tested the effects of gap (colonization hypothesis) and distance to parent tree (escape hypothesis) in the sarne experiment, and these were conducted on BCI-Panama (see Augspurger 1984, Schupp 1988).

Although density and distance effects on seed or seedling survi\'.al have been the focus of about 50 studies, the results have been highly variable. Thus the relative importance of these effects for individual trees and their population dynamics remains controversial (e.g., Janzen 1970, Connell 1971, Hubbell 1979, 1980, Howe and Smallwood 1982, Wright 1983, Clark and Clark 1984, Connell et al. 1984, Becker et al. 1985, Schupp 1988, Howe 1991, Forget 1993, Terborgh et al. 1993).

Another important point to consider is the scale at which the gaps affect seed dispersa! and survival within the forest Gaps of different sizes occur in the forest, and these may be located at different distances from one another, and from any fruiting trees. Fruiting ***Astrocaryum murumuru*** and ***Dipteryx micrantha*** trees occur both near (< 0-50m) and far (> 100m) from small and large gaps. Therefore, I examined the effect of distance from gaps on the seed and seedling dynamics of these two species.

This study was designed to test: a) whether the survival of ***Astrocaryum*** and ***Dipteryx*** seeds and seedlings is better in gap microenvironments than non-gaps (colonization hypothesis, Howe and Smallwood 1982, Orians 1982); b) whether súrvivorship of seeds and seedlings improves with distance from adult trees (escape hypothesis, Howe and Smallwood 1982); c) whether there are effects of distance from gaps on ***Astrocaryum*** seed survival, taking into account the density of seeds under the parent trees; d) whether ***Astrocaryum*** and ***Dipteryx*** seed and seedling survival is similar among gaps and at different spatial scales.

CHARACTERISTICS OF TIIE STUDY AREA. I conducted this study at the Cocha Cashu Biological Station, Manu National Park, Peru. Toe observations and experiments reported here were conducted between November 1991 and November 1993. Annual rainfall at Cocha Cashu is about 2000 mm and the annual mean temperature is 24 °C. A dry season of variable onset, duration and severity lasts from June to October, while the rainy season lasts from November to May. Toe Manu River flood plain is built on alluvial sediments carried out of the river's Andean sources. Toe forest has many emergent trees and a complex vertical structure (ferborgh 1985, Terborgh and Petren 1991, Gentry and Terborgh 1991). It is classified as a moist tropical flood plain forest (ferborgh 1983). Information on local plant and animal communities has recently been compiled in Gentry (1991).

ABOUT THE BIOLOGY OF THE PLANT SPECIES-

Information on the biology of the plant species is available in Chapter 1.

Methods

MEASURING GAP SIZE - Following Brokaw (1985), I considered a gap as an "opening in the forest extending down through all foliage levels to a height of 2 m above ground."

To sample the gap-size distribution in the study area, I measured 60 gaps found on each side of 5 parallel transects, located 200 m apart. Most tree-falls have an elliptical shape. Thus, I calculated gap area using the formula for an ellipse (A= 21tLW/4, where L and W are the lengths of the inajor and minor axes of the ellipse). From the 60 gaps mo t recently created, I randomly selected (using a random number table) sixteen recently formed gaps that ranged in area from 100 m^2 to 400 m^2. Plots for experimental seeds and seedlings were located in these (see experiment 1). Most of the 16 gaps appeared between December 1991 and May 1992 and were located within an area of 50 ha (pers obsv.). Neighboring gaps ranged from 50 m to 200 m apart, the extreme being about 1 km. Eight gaps were from multiple tree-fall gaps and eight from single tree falis.

I counted all extant *Astrocaryum* and *Dipteryx* seedlings found within each one of the sixty gaps in order to estimate the frequency and abundance of these species in gap habitats.

COLLECTING AND PREPARING EXPERIMENTAL SEEDS- Seeds for the experiments were collected at the beginning of the *Dipteryx* fruiting period (beginning of June). I washed the seeds in plastic basins and tested them for soundness before committing them to experiments. Soundness was judged from weight, absence of holes or scratches, ability to float, and hydrated kernel that did not rattle when the nut was shaken.

To distinguish experimental seeds from others present in the sarne locations, I marked all experimental seeds with an "e" using a permanent marker. Seeds were set out in the second week of June following the protocol described in the experimental designs of Experiments 1 and 2 (see below). Experimental seeds were checked weekly fo about 20 weeks. I searched intensively for the seeds within a radius of 3-5 m around the group of experimental seeds to verify whether any seeds had been moved by rodents from the original position in the experimental plots to a nearby location.

In a pilot experiment in which seeds marked with magnets were tracked by using a magnetic locator, I found almost all *Astrocaryum* seeds and the majority of the *Dipteryx* seeds preyed upon by mammals (rodents) (see chapter 1). Although seed removal is not always equivalent to seed predation (Forget and Milleron 1992), it has been found that for several tropical tree species, seed removal corresponds well to seed predation (Rankin 1978, Schupp 1989).

Under conditions of food shortage, scatterhoarding by secondary dispersers was probably a rare event (Forget and Millero 1992). Secondary dispersers such as spiny rats and agoutis, which are the main seed dispersers and predators of *Astrocaryum* and *Dipteryx,* scatterhoard seeds mostly when seeds are very abundant (Smythe 1989, Forget 1991, Forget and Milleron 1992).

EXPERIMENT 1- SEED AND SEEDLING SURVIVAL IN GAPS VS. SHADY UNDERSTORY

EXPERIMENTAL DESIGN OF SEED SURVIVAL: To investigate the effects of gaps on seed survival I delimited a 10 x 10 m plot within each experimental gap in the crown and bole zones and in the understory beneath and farther from an adult tree.

I first subdivided each 10 x 10 m plot into one hundred $1 m^2$ subplots in which the central part of each subplot (0.50 x 0.50 m) was located. Toe experimental seeds were placed in these central locations. I used a random number table to select the positions of the subplots to be used. Toe experimental seeds were then randomly assigned to 8 experimental subplots of 0.50 x 0.?0 m within each gap, and 8 subplots in the nearby forest understory.

I set out 8 seeds in four randomly located 0.50 x 0.50 m subplots, in each of the following microsites: a) crown zone of gap, b)bole zone of gap; c) forest understory beneath an *Astrocaryum* or *Dipteryx* tree; and d) forest understory > 20 m from an adult *Astrocaryum* tree and > 40 m from an adult *Dipteryx*. Toe latter distances were attempts to avoid the influence of conspecific trees. Toe subplot dimensions were intended to simulate the piles and caches produced by primary and secondary mammalian dispersers. Toe seed number used per plot (8) is within the range I observed for spiny rat and agouti caches of *Astrocaryum* and *Dipteryx* seeds, and for bat roosts located in the understory *(Dipteryx* only). I checked each treatment for seed survival for 20 weeks.

STATISTICAL ANALYSIS- For the seed survival data of Experiment 1, Cox models were fitted by using the Cox Proportional Hazard Regression procedure available in Splus (1991 see chapter 1, page 12 for details). Since some seeds were surviving at the end of the experiment, I also analyzed the maximum time of survivorship using analysis of variance (ANOVA). In this analysis, the response variable was the number of weeks seeds survived. Toe effects of the sarne four treatments on this variable were also analyzed. Analysis of Covariance (ANCOV A) was used to investigate gap size effects on maximum time of seed survivorship.

SEEDLINGS EXPERIMENTAL DESIGN: Seedling establishment and survival is the next phase in natural regeneration after seed dispersa! and germination. To simulate the colonization of gaps, I transplanted experimental seedlings of ***Astrocaryum*** and ***Dipteryx***, comparing their survivorship within gaps and in the understory. I used the sarne gaps as in Experiment 1. I transplanted 512 experimental ***Astrocaryum*** seedlings and 128 ***Dipteryx*** seedlings. Toe ***Astrocaryum*** seedlings were collected under mature trees located > 1 km from the experimental area. Toe seedlings used had recently germinated, and still had the exocarp attached to their stems. Toe first leaf of most of them had just started to open. I kept them for a week before transplanting them to the experimental sites at the beginning of July. ***Dipteryx*** seeds were germinated within plastic bags kept within a protected enclosure. Fewer ***Dipteryx*** seedlings were obtained than ***Astrocaryum*** seedlings. Consequently, only four gaps were used in the analysis of ***Dipteryx*** seedling survival. I transplanted the seedlings to experimental sites at the end of September.

Seedlings were transplanted in groups of four per 1 m^2 subplot. Treatments were the sarne as in Experiment 1, with 2 replicates per treatment. I used the sarne 16 gaps as in Experiment 1 for ***Astrocaryum*** seedlings, but only four of them for ***Dipteryx*** seedlings (dueto the limited number of seedlings available). Seedlings, with soil from a cooking hearth, were transported to the experimental sites in small plastic bags. Before transplanting, I slit the plastic bags along the sides and bottom. After the seedling had been planted, the plastic bags were removed to avoid physical darnage to the roots. Only seedlings in good condition and without leaf damage were used in the experiments.

Experimental seed.lings were censused after one week in the field. A few seedlings died during the first week, but were replaced by new ones.

STATISTICAL ANALYSIS-I used two different statistical approaches. I used standard statistics to analyze part of the tails of survival curves and the technique of survival analysis to analyze the complete survival curves (see page 12). For the first set of analyses, I used different response variables the number of seedlings surviving after a given number of weeks. I used analysis of variance (two-way ANOVA) available in SYSTAT (Wilkinson 1991) to compare seedling survival under different treatments and their interactions. Seedling survival of both plant species was then analyzed at different spatial scales or locally in a given gap site (the four treatments) and arnong gap sites in the forest using two-way ANOVA models.

EXPERIMENT 2- EFFECTS OF DISTANCE FROM GAPS ON *Astrocaryum* SEED SURVIVAL

Gaps appear haphazardly in the forest. Distance between gaps and between any given gap and the nearest fruiting tree of a particular species can therefore be expected to vary widely. Here, I investigated the effects of distance of gaps from fruiting *Astrocaryum* trees on *Astrocaryum* seed survivorship. During the sarne days the experimental seeds of Experiment 1 were set in the field, I registered naturally occurring seeds already present around the adult tree trunks by delimiting five plots of 30 x 30 cm under 15 mature *Astrocaryum* palms located near (20-30 m) each of the 16 experimental gaps (sarne trees from treatment 3 of Experiment 1). I used colored tooth picks to demarcate the 30 x 30 cm plots. These were called "natural seed densities" and were censused weekly for 20 weeks for survival. Toe experimental seeds from the four treatments in Experiment 1 were censused concurrently.

I also censused experimental and naturally occurring seeds in five plots of 30 x 30 cm plots located under 10 adult trees located far (> 100 m) from gaps. Each of these 10 trees was located at least 30 m from any other of the sarne species, and at least 100 m from a gap.

I investigated seed survival near and far from gaps by: 1) comparing survival curves using Cox Proportional Hazard Regression for survival analysis, and 2) comparing the number of weeks the experimental seeds survived under 15 experimental trees near gaps, and under 10 parent trees far from gaps. I baseei survivorship on the means of the five plots under each of the 25 trees. Analysis of covariance (ANCOVA) from SYSTAT (Wilkinson 1991) was also used to test: 1) whether seed survival was higher near or far from gaps after taking into account the covariate "natural seed density under parent trees," and 2) whether there was a gap size effect on seed survival using the gap area as covariate. Values of the dependent variables were square-root transformed when necessary to normalize their distributions.

Results

GAP SIZE DISTRIBUTION - Toe gap size distribution in the study area follows a negative exponential (Figure 2). Toe mean gap area was 320 m^2 (range 23.6 - 1189.9 m^2; N=60).

SEED ANO SEEDLING SURVIVAL IN GAPS VERSUS CLOSED CANOPY FOREST-

In this section I present the descriptive results of the number of seeds and seedlings surviving at the end of the gap Experiment 1. Few ***Astrocaryum*** experimental seeds survived to the end of the experiments. After 20 weeks (five months) on the forest floor, the number ofremaining seeds was 53 (2.6 %). Of that total, 41 seeds (77.4%) survived within gaps and 12 seeds (22.6%) survived in the forest shady understory. A total of 162 (12.6%) ***Dipteryx*** seeds remained intact at the end of the experiments. Of those, 95 seeds (59%) survived within the gaps, and 67 seeds (41.35%) remained intact in the understory. At the end of the experiment only five ***Astrocaryum*** and two ***Dipteryx*** seeds were germinating.

SEEDLING SURVIVAL-A large number (454) of ***theAstrocaryum*** seedlings (88.67%) were still alive at the end of the experiments (after 16 weeks) in 1992. Of those, 233 seedlings (51.3%) were alive within gaps and 221(48.7%) seedlings in the shady understory.

In the whole experiment, a total of 87 ***Dipteryx*** seedlings (67.8%) remained after 10 weeks. From those, 45 (51.7%) seedlings were in the gaps and 42 (48.3%) seedlings were in the understory. Since most of the seedlings that did not survive disappeared from the plots, I suspect they were completely brow ed by herbivores.

ln September 1993, one year after the *Astrocaryum* seedlings were placeci in the experimental plots (Experiment 1), I could find the seedlings in only 5 gap sites because their tags were missing and the gap vegetation was much more closed. Therefore the percentages of seedling survival in 1993 reporteei here are relative to the total initial numbers of seedlings placeci in the 5 gap sites. From the initial number of 192 *Astrocaryum* seedlings placeci in the *5* gaps, 121(63%) were still alive at the end of the experiment. From those (121), 65 (33.8%) seedlings were alive within gaps (crown and bole zones combined) and 56 (29.2%) seedlings alive in the understory (sum of beneath and farther from adult trees treatments).

I have complete data for only 3 gap sites for *Dipteryx* seedlings. From the initial number of 96 seedlings placeci in the 3 gap sites, 34 (35.4%) seedlings were alive within gaps and only 8 (4.2%) seedlings were alive in the shadeci understory.

TREE-FALL GAPS AS A COMPONENT OF SPATIAL HE1EROGENEITY AFFECTING SEED AND SEEDLING SURVIVAL

GAP EFFECTS ON SEED AND SEEDLING SURVIVAL IN THE FOREST- ln Experiment 1, I analyzeci seed and seedling survival on a much larger scale by comparing their survivorship among gap sites. I compareci gap sites, using two treatments within gaps (bole and crown) and counterpart treatments in the forest interior (beneath and far from an adult conspecific). The analysis may show how the distribution of an environmental factor at large sp·atial scales, in this case gap sites, affects seed and seedling survival in the forest

When entire survival curves were compareci using survival analysis (Cox model), *Astrocaryum* and *Dipteryx* seeci survivorship followed different patterns at small scales (within a gap site and the corresponding understory sites), but similar patterns at larger spatial scales (among gap sites in the forest). *Astrocaryum* seed survivorship differed significantly among gap sites, but not between the four experimental treatments (fables 1, 3, and Figures 3 and 4). *Dipteryx* seed survivorship also differed significantly among gap sites and between the four treatments. *Dipteryx* seed survival was higher within gaps (crown and bole zone) and also farther from the adult target trees in the closed understory (fables 1 and 4 and Figures 3 and 4).

When maximum time of survival (number of weeks) was used, there were significant differences in the number of weeks *Astrocaryum* seeds survived among the 16 gap sites, but not among the four treatments. However, the interaction between treatments and gap sites was also significant (fable 3). Toe sarne patterns of survival were shown by *Dipteryx* seeds. Toe number of weeks *Dipteryx* seeds survived was significantly different among gap sites. There was also a significant interaction between treatments and gap sites (fable 4).

SEED SURVIVAL IN RELATION TO DISTANCE TO A GAP

In Experiment 2, I investigated whether *Astrocaryum* seeds placed beneath trees located close to gaps had higher survivorship than those placed beneath trees located far from gaps. Survival of *Astrocaryum* experimental seeds was higher under the adult trees near gaps than far from gaps (Figure 5a). Under adult trees near gaps, about 50% of the seeds survived through the second week, while only 28% of the seeds under adult trees far from gaps did so.

No *Astrocaryum* seeds survived longer than 9 weeks far from gaps, but about 5% of seeds survived to the 20th week under trees near gaps (Figure 5 a). Naturally occurring *Astrocaryum* seeds showed the sarne pattem of survivorship (Figure 5 b).

Analysis of the whole survival curves confirmed that *Astrocaryum* seed survival was significantly higher near gaps than far from gaps (Cox regression, coef.= -0.335; z=-8.49; p<00000l; see also Figure 5).

ln addition, I used standard parametric statistics, analysis of covariance (ANCOVA), to investigate whether distance from gaps affected *Astrocaryum* seed survival. Toe response variable was the number of weeks seeds survived (NUWK.SUV). The categorical variable was treatments (near and far from gaps), and the covariate was naturally occurring density of seeds (NATDENS) under adult trees in both treatments.

Before I ran the ANCOVA, I first tested whether there was an interaction between NATDENS and treatments. The interaction was insignificant (F=0.005; DF= l; p=0.946). Seed survival showed highly significant differences between treatments. *Astrocaryum* seeds survived significantly longer near gaps than far away from gaps (Table 2 and Figures 5, 6 and 7).

GAP EFFECTS ON SEEDLING SURVIVAL

Here I simulated the colonization of gaps with transplanted experimental seedlings of *Astrocaryum* and *Dipteryx* seedlings in gaps compared to paired sites in the understory (under and away from 16 *Astrocaryum* and 10 *Dipteryx* trees located near gaps) using the sarne experimental design and tree-fall gaps as in the experiments with seeds.

In all the experimental groups of ***Astrocaryum*** seedlings, at least one seedling survived until the end of the experiment. Therefore, I used as response variable the mean number of seedlings surviving at the 15th week. For survival of ***Astrocaryum*** seedlings, the results were similar to those found for ***Astrocaryum*** seeds, with significant differences among gap sites, but not between gap and understory (treatments). Interactions between gap sites and treatments were significant for ***Astrocaryum*** seedling survival (Table 3). ***Astrocaryum*** seedling survival after one year was not significantly different between gap sites and between gap and understory treatments (Table 3).

For ***Dipteryx*** seedlings, I used as response variable the number of weeks at least one of the seedlings from one of the experimental groups of four seedlings survived. Survivorship was compared under the same treatments and sites used for experimental seeds. Seedling smvival was also compared among experimental gap sites. After 12 weeks, there was a significant difference among experimental gaps, but not among the four treatments. After one year, however, the number of ***Dipteryx*** seedlings still alive was significantly higher in gaps than in the ui:iderstory. Interactions between gap sites and treatments were not significant (Table 4).

GAP SIZE EFFECTS ON SEED AND SEEDLING SURVIVAL

I also investigated whether the size of experimental gaps affected seed and seedling survival of both plant species: There were no significant differences in the number of weeks ***Astrocaryum*** seeds survived within gaps of different sizes (Table 5). A highly significant difference was found for ***Dipteryx*** seed survivorship however (Table 5). ***Dipteryx*** seeds survived longer in small than in large gaps. Variation in gap size had no important effects either on the final number of ***Astrocaryum*** seeds and seedlings surviving after 15 weeks in the 16 gaps, or on the number of weeks *Dipteryx* seedlings survived in 4 gaps (Table 5).

Discu ion and conclusions

Seeds of *Astrocaryum* and *Dipteryx* survive better near and within tree-fall gaps than in the shady understory far from gaps. Seedlings of both plant species grow faster in well-lit environments (unpub. data, see also Fetcher et. al. 1987). Toe performance of seedlings may be enhanced in gaps, possibly allowing higher rates of population recruitment

Toe survival probability of either plant species, and possibly of any plant species in the forest, increases with time as the number of seeds remaining to be eaten decreases. Differences in seed-survivorship among treatments over the five-month experiment were significant for *Dipteryx*, and among gap sites for *Astrocaryum* andDipteryx.· Variability of seed predation in time and space will certainly contribute to variation in the number of seeds present at the time of formation of any given gap (Grubb 1977). Although this argument may be more valid for species with small seeds that produce seed banks, it may also apply to large-seeded species with short but variable dormancy periods, such as *Dipteryx* and *Astrocaryum*.. ln both species, some viable seeds can be found one year after dispersa! from the parent tree (Pers. Obs).

Toe fact that *Astrocaryum* -seed survival curves representing the four treatments did converge at some time indicates that seed survival is not strongly habitat dependent over the short run (few months) (Figures 3 and 4). However, difference::s in the physical environments of understory and gap may be important in determining seed survival under biological interactions, such as predation by animais (Chapter 1). How thoroughly rats, agoutis, squirrels and other seed predators search the forest floor may be dependent on the type of habitat (gap or understory). Post-dispersal seed predation by mammals on the two plant species is demonstrated here to be very high. About 50% of the seeds of both plant species were attacked by mammalian and or insect predators within two to six weeks after they were set out on the forest floor (Figures 3 and 4).

This study was conducted during a year of relatively good fruit production by the two plant species. Seed predators might thus have been satiated (Janzen 1971a). Even given the high rates of seed predation recorded in the experiments, I observed many apparently viable seeds on the forest floor, suggesting that predators had been satiated.

After just 10 weeks, the great majority of *Astrocaryum* seeds had been removed, and by the end of the study, up to 97% had disappeared. Predation on *Dipteryx* seeds was also high. These results support many claims in the literature that large-seeded species experience very high losses of seeds to seed predators (Watt 1947, Janzen 1970, 1971, Howe and Smallwood 1982). High leveis of seed predation have also been found in congeneric species in other neotropical areas (*Astrocaryum paramaca* in French Guiana, Forget 1991; *Astrocaryum standlaenyum* and *Dipteryx panamensis* in Panama, De Steven and Putz 1984, Smythe 1989, Forget 1993; *Dipteryx panamensis* in Costa Rica, Clark and Clark 1984; and *Astrocaryum mexicanum* in Mexico, Velasquez and Martinez-Ramos 1991).

Predation by rodents on seeds and seedlings was found to be higher in gaps than in the understory both in Panama for *Faramea occidentalis,* and in Costa Rica for the palm *Welfia georgii* (Schupp 1988, and Schupp and Frost 1989). My results with *Dipteryx* seeds are in accord with these published reports, but in contrast, *Astrocaryum* seeds survived better in the shaded understory, especially close to gaps. Such differences in the effect of gaps on seed survival could be due to differences in the abundance of rodents between sites and to differences in their behavior toward different plant species. The large rodents at BCI are released from predation by top predators. They may consequently be uninhibited in using open areas such as gaps.

Rates of gap fonnation (ca 1% per hectare/year) may be similar at BCI and Cocha Cashu. However, large gaps appear to be more common at Cocha Cashu (Figure 2), possibly leading to greater environmental heterogeneity. Toe higher frequency of larger gaps at Cocha Cashu may be dueto higher soil fertility. Higher nutrient availability and input in the plant biomass produce larger trees and consequently larger gaps when the trees fall. ln studying gap frequencies in Amazonian Ecuador, Kapos et al. (1990) found that a forest in a less fertile site had a smaller percentage of area in gaps (1.4 %) than a forest in a fertile site (5.1 %). A greater number of large gaps in a given area make the . distances among gaps shorter, producing more complex understory vegetation in response to the presence of gap edges. Rodents might avoid areas near gaps if they offer better conditions for detection and attack by mammalian and avian predators (raptors and owls). Attack by bruchids, however, is likely to be independent of the risk of exposure to vertebrate carnivores.

THE GAP DISTANCE EFFECTS ON SEED SURVIVAL

Severa! recent studies have examined seed survival in gaps relative to that in the shaded understory (see Webb and Wilson 1985, Wilson 1988, Schupp 1988). The available information suggests that gap effects on seed survival depend on plant species (Augspurger 1984, Wilson 1988, Schupp 1988). Although a majority of tropical tree species may depend on gaps for reg neration (Hartshom 1978), in the life cycle of a given plant species the importance of gaps will depend not only on dispersai and seed size, but also on the behavior of seed predators (Janzen 1971a, b, Price and Jenkins 1986, Forget 1990, 1993). The phenological behavior of other plant species near a given tree could also be important in attracting or not attracting seed predators during the fruiting period of the focal tree.

My finding that *Astrocaryum* seeds survived better near and inside gaps suggests that rodents may remove seeds from gaps and store them in the understory nearby. These sites may provide temporary safe places to open relatively hard seeds like those of *Astrocaryum* . Rodents may use the intricate and complex gap ecotone, which is composed of limb and vine tangles, as shelter and food storage sites. Pehaps that is why *Astrocaryum* seed survival was higher near gaps. If rodents use these ecotones more, then I would expect higher seed survival there. Survival of scatterhoarded seeds results from rodent forgetfulness. Rodents may forget (or ignore) stored seeds when a more prefered species comes into fruit within their home ranges (Smythe 1989).

Other seed predators, such as peccaries, have quite distinct behavior. Peccaries cover large areas, and do not transport or store seeds. Thus they act as strict seed predators (Kiltie 1981, Bodmer 1991). Agoutis, squirrels and other rodents play dual roles as dispersers and predators of seeds (Emmons 1982, 1990). Because rodents have much smaller home ranges than peccaries, they may scan more often in a given area of forest. Also, because their food requirements are much smaller, rodents can profitably search for low density post-dispersal seeds. Then the overall impact of rodents on *Astrocaryum* seed survival is less patchy in the forest than the impact of Peccaries. Such differences might explain why there were significant differences among but not within gaps in seed survival. Generally greater survival of *Dipteryx* seeds relative to *Astrocaryum* seeds may be related to the greater difficulty of extracting the kemel. *Dipteryx* seeds have fewer species of mammalian predators than *Astrocaryum* seeds. It has been found in Panama, for example, that *Dipteryx panamensis* seeds account for

78% of the diet of the squirrel ***Sciurus granatensis*** (Glanz 1984). Its possible that squirrels avoid gaps. Squirrels ***(Sciurus spadiceus)*** were frequently observed along the trail system at Cocha Cashu. They seem to prefer understory areas where lianas are abundant because they often use them for horizontal locomotion. Newly formed gaps do not have many lianas at a relatively safe height from the ground because they tend to be pulled down with the falling tree. It is possible then that the greater survival of ***Astrocaryum*** seeds near gaps can be attributed to avoidance of these areas by ***S. spadiceus*** .

GAP SIZE VARIATION AND REGENERATION OF *Astrocaryum* and *Dipteryx*-

I provide here the first data on gap sizes at Cocha Cashu. Because gap margins are hard to define, I used a conservative method to estimate gap area (Brokaw 1985). But even using a conservative method, I might have overestimated the size of some gaps. The data should be verified with another set of estimates. The mean gap size I recorded at Cocha Cashu is at least three times that in other neotropical forests. For example in Costa Rica, Hartshom (1978) found a mean of 89 m^2, while at Cocha Cashu I found a mean 320 m^2. Toe Cocha Cashu forest also seems to have relatively fewer small gaps.

I found that gap size affected the survival of ***Dipteryx*** seeds, but not of ***Astrocaryum*** seeds and seedlings (Table 5). Naturally occurring ***Astrocaryum*** seedlings were found in 84% of gaps surveyed and naturally occurring ***Dipteryx*** seedlings in 13%. The difference may simply reflect the much higher density of ***Astrocaryum*** seedlings than of ***Dipteryx*** seedlings on the forest floor in general.

The results also indicate that although these two plant species show good short-term survival in the shade environment, they may opportunistically benefit from gaps.

A weak but significant negative relationship between the number of *Astrocaryum* seedlings present within gaps and gap size suggests that there may be a limited range of gap sizes optimal for establishment However, it is very clear that *Astrocaryum* regenerates under a wide range of conditions because plants of all sizes can be found nearly everywhere in the forest and at relatively high abundance (Kiltie 1981).

Low rates of seedling survival in gaps were found for *Dipteryx panamensis* in Costa Rica (Clark and Clark 1987). However, the authors found few large juveniles and small adults in their study area, and concluded that *Dipteryx panamensis* regeneration might be a relict of past regional disturbances. At Cocha Cashu, I found the sarne pattem: few saplings over 1.5 m in height, two sub adults with 23-26 cm trunk diameter, and adults up to 173 cm dbh. This suggests the existence of a demographic bottleneck in *Dipteryx micrantha* regeneration.

DISPERSAL AND PLANT RECRUITMENT

It has been assumed that large-seeded species may be characterized by limited seed dispersai (Janzen 1971, Harper 1977, Howe and Smallwood 1982). The limitation in seed dispersai is more likely to be due to post-dispersal predation than the ability of animais to move seeds. For *Dipteryx* this generalization does not seem to hold because bats, as primary dispersers, can move seeds far away from the source. *Dipteryx* seeds have been found under bats roosts as much as 500 m from the nearest adult tree (pers. com. Monica Romo). Secondary dispersai by terrestrial rodents occurs on a more limited spatial scale (unpl.res.ults, and see Forget and Milleron 1992). This statement may be valid for both *Astrocaryum* and *Dipteryx* at Cocha Cashu.

Seeds of both tree species can be transported by a large assemblage of primary and secondary dispersers, including monkeys, macaws, marsupiais, bats, squirrels, rats, agoutis, etc. (see Bonacorso et.al 1980, Emmons 1982 for *Dipteryx,* Forget 1991a for *Astrocaryum).* Such a high diversity of d.ispersers, each with its individual behavioral responses to changes in seed availability and other factors, creates a complex and ever-changing dispersa! scenario. To know which of the two plant species would be more favored by gaps in the long run, one would .need infonnation on the predictability and frequency of gap fonnation, and which of the two plant species would be more affected by these components of disturbance.

Successful recruitment of *Astrocaryum* and *Dipteryx* , and pehaps by the majority of large-seeded tree species at Cocha Cashu, is a complex matter. Multiple factors in addition to dispersa! operate at different spatial scales. Some of these factors are: local variation in the distribution and abundance of the mammalian vectors, population fluctuations of insect predators, occurrence of flooding, spatial heterogeneity created by gaps, year to year variation in phenological behavior, <;fegree of the effects ofseedling density and distance from parent trees on seedling survivaJ.;varying degrees of seed palatability, and tolerance and physiological responses of seeds and seedlings to occasional long droughts (Janzen 1969, 1970, 1971a,b, 1978, Grubb 197-7, Denslow 1980, Bazzaz 1984, Smythe 1986, Horvitz and Schemske 1986, Hubbell and Foster 1987, Howe et al. 1985). However, as this study showed, seed and seedling density and their proximity to conspecific adults, the amount of incident light, the amount of understory vegetation cover, leaf litter thickness, and distance to a gap and gap size,. are all important factors affecting the population recruitment of *Astrocaryum andDipteryx* at the Peruvian Amazon forest.

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Table 1. Survival of *Astrocaryum* and *Dipteryx* seeds in relation to: sixteen gap sites and four treatrnents (gap crown and bole zones and beneath and farther from an *Astrocaryum* or *Dipteryx* target tree located in the continuous understory near the experimental gap) (Cox Proportional Hazard Regression).

Parameter	DF	Estimate (SE)	z	Sig. level
Astrocaryum +				
Among gap sites	15	0.028 (0.005)	5.41	***
Between treatments	3	0.029 (0.020)	1.42	ns
Within zones	255	-0.004 (0.020)	-0.19	ns
Dipteryx++				
Among gap sites	9	-0.020 (0.006)	-6.57	***
Between treatments	3	0.071 (0.027)	2.67	***
Within zones	159	-0.003 (0.027)	-0.09	ns

***, $p<0.0001$; **, $p<0.001$; *, $p<0.05$; ns, not significant.
+Likelihood ratio test=314 on 3 DF, $p<0.00001$; ++ Likelihood ratio test=19.1 on 3 DF, $p<0.00026$

Table 2. Results of Analysis of Covariance (ANCOVA) on the number of weeks *Astrocaryum* seeds survived under target trees near and far from gaps, taking into account the covariate natural seed density under those target trees

Source of Variation	SS	DF	MS	F	p
Natural seed density	24.746	1	24.746	1.486	0.236
Distance from gap (Nearx Far)	169.455	1	69.455	10.173	0.004
Error	366.456	22	16.657		

Table 3. Results of two-way Analysis of Variance (ANOVA) of response variables, 1) number of weeks *Astrocaryum* seeds survived in sixteen gap sites; 2) number of *Astrocaryum* seedlings surviving after fifteen weeks in sixteen gap sites; 3) number of *Astrocary* seedlings alive after one year in tive gap sites. Categorical variables for ali three response variables above were four treatments: a)seedlings placed in crown, and in b)bole zones in gaps, and in the understory e) beneath and d) far away from an adult tree. See methods for further details.

Source of variation	SS	DF	MS	F
1- *Astrocaryum* seeds				
Gap site	6217.340	15	414.489	34.093***
Treatments	153.418	3	51.139	4.630ns
Gap sites*treatments	3594.395	45	79.875	6.570***
Error	2334.250	192	12.158	
2- *Astrocaryum* seedlings after 15 weeks				
Gap sites	22.719	15	1.515	5.385***
Treatments	0.531	3	0.177	0.630ns
Gap sites*treatments	34.219	45	0.760	2.704***
Error	18.219	64	0.281	
3- *Astrocaryum* seedlings after 1 year				
Gap sites	0.635	4	0.159	0.710ns
Treatments	1.176	3	0.392	1.752ns
Gap sites*treatments	2.487	12	0.207	0.541ns
Error	4.477	20	0.224	

*** p<0.0001; ** p<0.05; ns = not significant. Data were root-squared transformed when necessary to approximate normal distribution.

Table 4. Results of two-way Analysis of Variance (ANOVA) of response variables, 1) number of weeks ***Dipteryx*** seeds survived in ten gaps; 2) number of weeks ***Dipteryx*** seedlings ative after twelve weeks in four gap sites; 3) number of ***Dipteryx*** seedlings ative after one year in three gap sites. Categorical variables for all three response variables above were four treatments: seeds placed in a)crown, b)bole zones in gaps, and in the understory e) under and d) far away from an adult tree. See methods for further details.

Source of variation	**SS**	DF	MS	F
1-Dipt ryx seeds				
Gap sites	224.925	3	74.975	5.542***
Treatments	2767.725	9	307.525	22.731***
Gap sites*treatments	867.825	27	32.142	2.376**
Error	1623.500	120	13.529	
2-Dipteryx seedlings after 12 weeks				
Gap sites	73.594	3	24.975	785.000***
Treatments	0.094	3	0.031	1.000ns
Gap sites*treatments	0.281	9	0.031	1.000ns
Error	0.500	16	0.031	
3- ***Dipteryx*** seedlings after 1 year				
Gap sites	3.506	2	1.75	6.929**
Treatments	3.458	3	1.153	4.557**
Gap sites*treatments	2.917	6	0.486	1.921ns
Error	3.036	12	0.253	

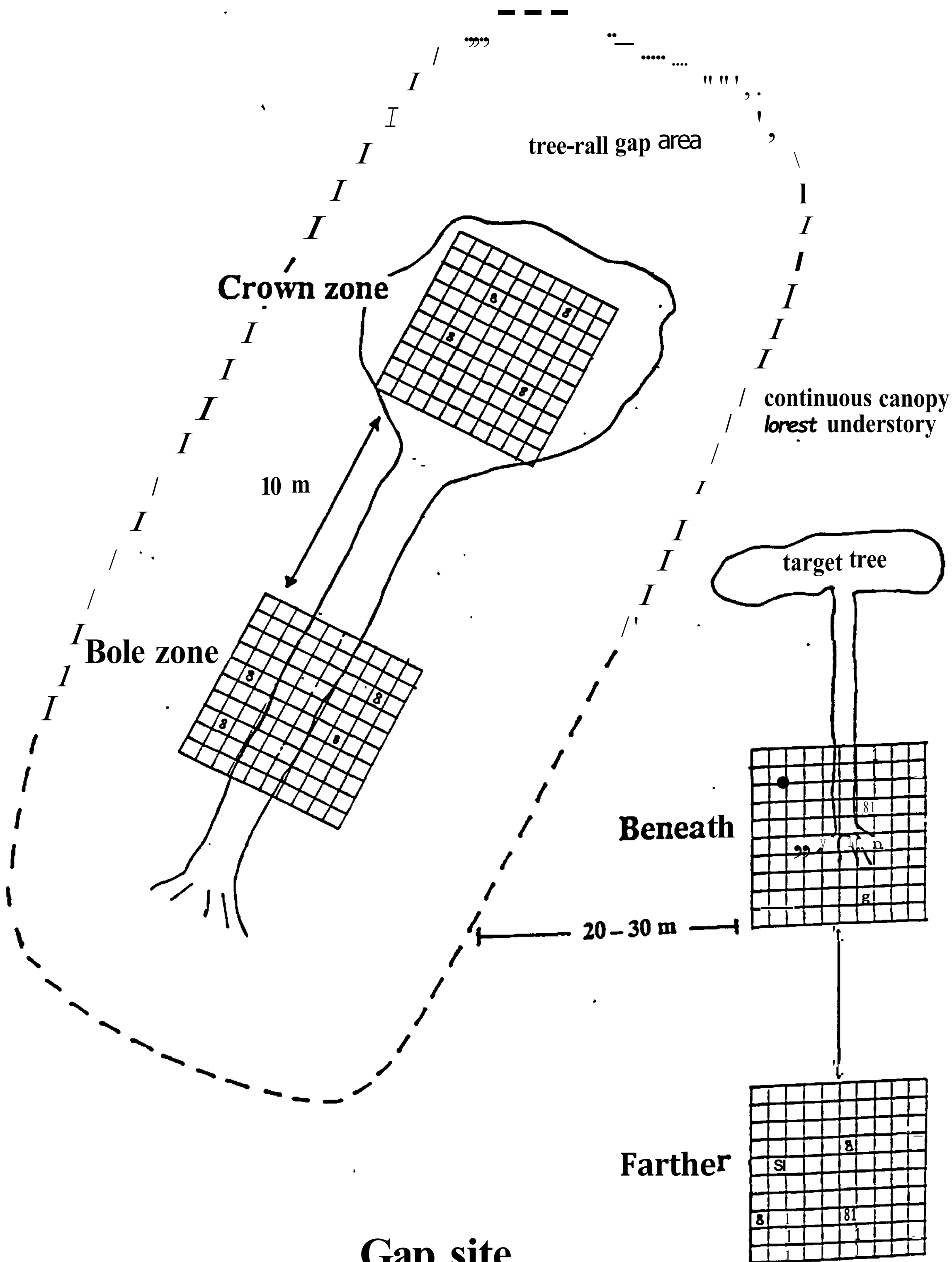
*** p<0.0001; ** p<0.05; ns = not significant . Data were root-squared transformed when necessary to approximate normal distribution.

Table 5. Results of Analysis of Covariance (ANCOVA), using the covariate gap size, of response variables: 1) number of weeks ***Astrocaryum*** seeds survived in sixteen gaps; 2) number of ***Astrocaryum*** seedlings surviving after fifteen weeks in sixteen gaps; 3) number of weeks ***Dipteryx*** seeds survived in four gaps; 4) number of weeks ***Dipteryx*** seedlings survived in four gaps. Categories for all four response variables above were the two experimental treatments: seeds placed in a)crown and b)bole zones within each gap. See methods for further details.

Source of variation	SS	DF	MS	F
1- ***Astrocaryum*** seeds				
Treatments	56.867	1	56.867	1.068n
Gap size	0.018	1	0.018	0.000ns
Error	6546.419	123	53.223	
2- ***Astrocaryum*** seedlings				
Treatments	0.016	1	0.016	0.881ns
Gap size	0.047	1	0.047	0.068ns
Error	42.047	61	0.689	
3- ***Dipteryx*** seeds				
Treatments	19.013	1	19.013	0.666ns
Gap size	450.357	1	450.357	15.785***
Error	2196.818	77	28.530	
4- ***Dipteryx*** seedlings				
Treatments	0.000	1	0.000	0.000ns
Gap size	1.104	1	1.104	0.423ns
Error	33.896	13	2.607	

*** $p<0.0001$; ns = not significant ($p<0.10$). Data were ro t-squared transformed when necessary to approximate normal distribution.

Figure 1. Field experimental design for Astrocaryum and *Dipteryx* seeds and seedlings, showing the four treatments. The two treefall gap treatments were (a)crown zone, or at area of the created gap covered by the fallen tree crown; and (b) bole zone, or on both sides of the fallen tree trunk in the gap site (area created by falling trees, the area delimited by the dash line). The two continuous forest understory treatments were, seeds placed on the ground (e) beneath an adult target tree and on the ground (d) farther away from the target tree located 20-30 m from a gap. There were four groups of eight seeds and two groups of four seedlings for each one of the four treatments. This entire design was replicated at sixteen gap sites for *Astrocaryum* seeds and seedlings and ten gap sites for *Dipteryx* seeds and five gap sites for *Dipteryx* seedlings. Toe area within the dash line represents the treefall which produced the gap. See methods for further details.



tree-rall gap area
Crown zone
10 m
Bole zone
continuous canopy
lorest understory
target tree
Beneath
20 – 30 m
Farther

Gap site

Figure 2. Gap size distribution at Cocha Cashu Biological Station, Manu National Park, Peru, 1992, (N = 60).

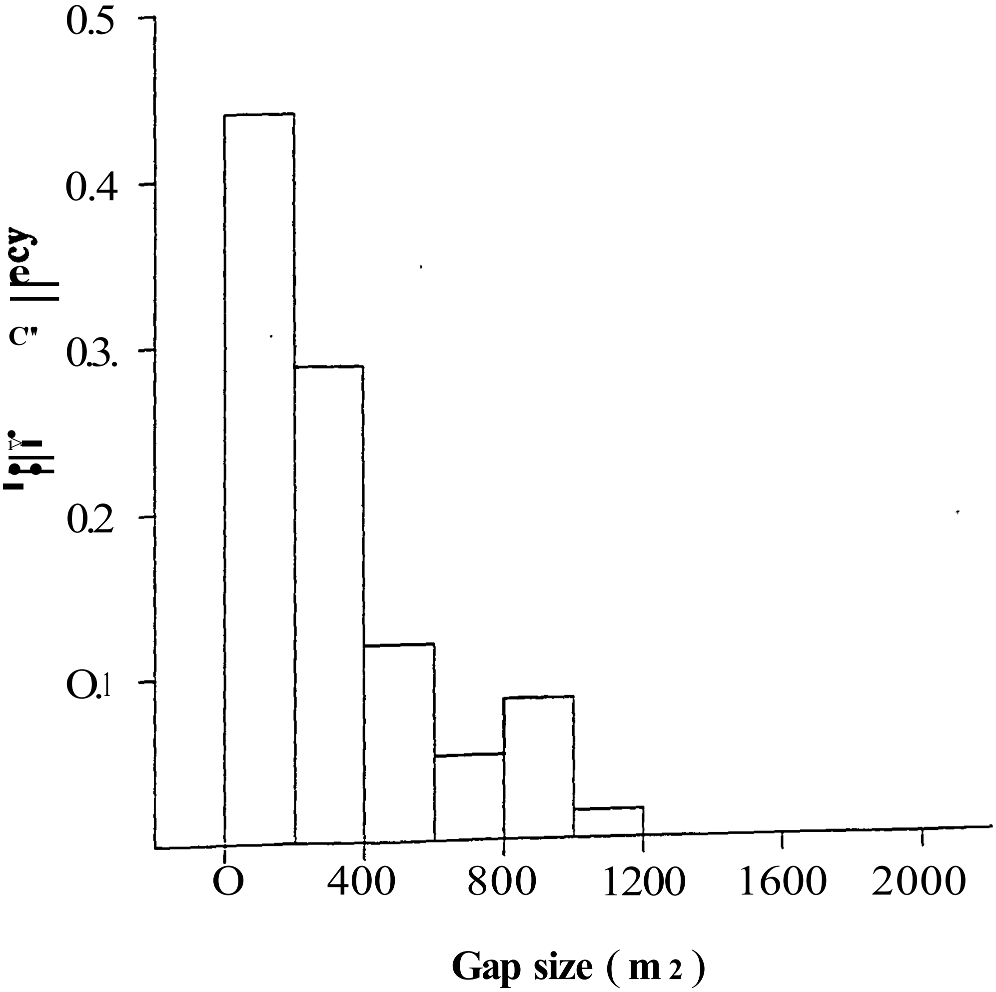
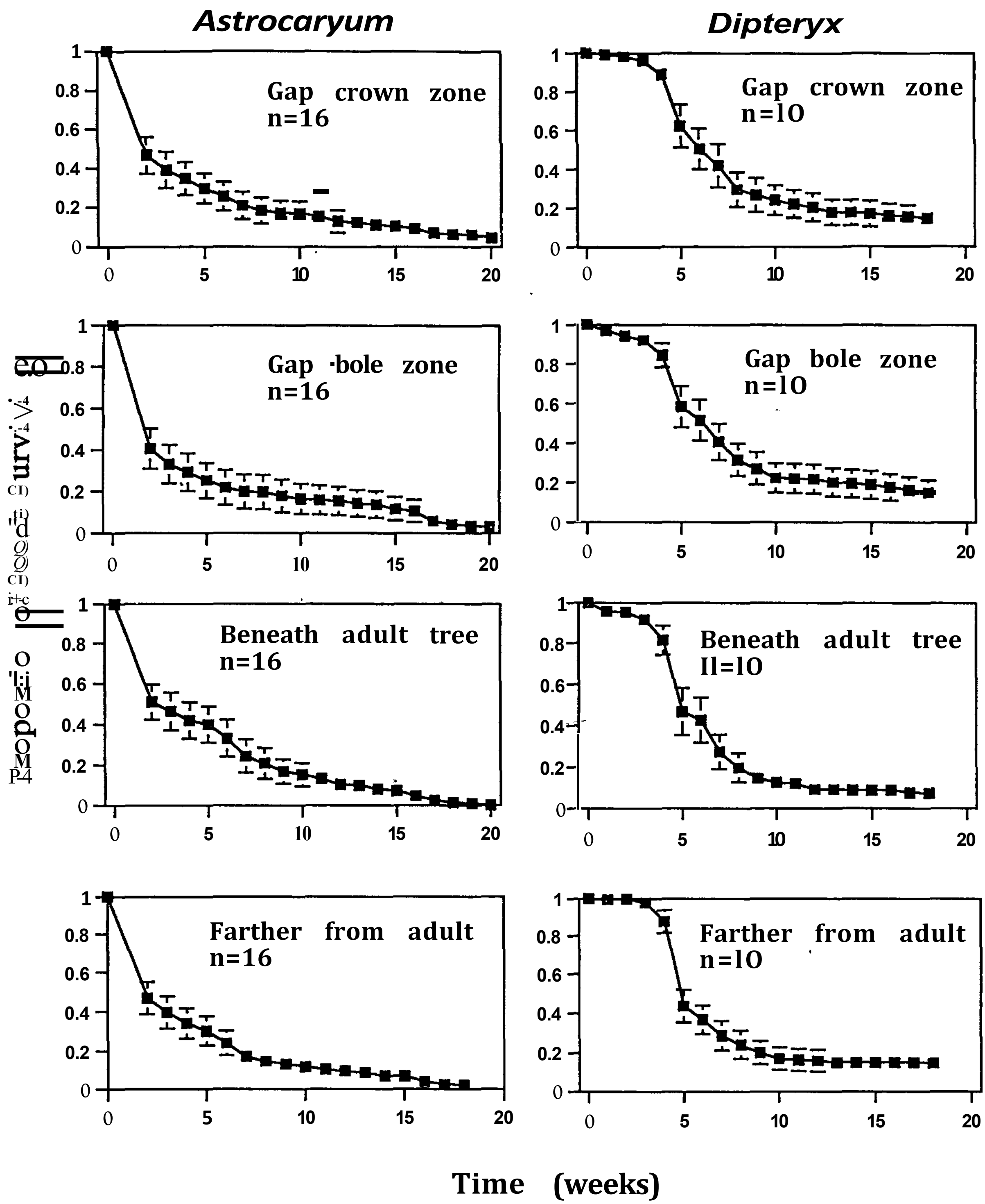

0.5
0.4
0.3
0.2
0.1
0
400
800
1200
1600
2000
Gap size (m2)

Figure 3. M an proportion of a) *Astrocaryum* and b) *Dipteryx* seeds surviving at weekly intervals, at all sixteen gaps sites *(Astrocaryum)*, and at all ten gap sites *(Dipteryx)*, in two gap zones (crown and bole and two understory zones, under and >20m away from an adult palm, located in the understory about 20-30m from the gap. The four graphs on the left are for *Astrocaryum* seeds and the four on the right for *Dipteryx* seeds. Squares are means and vertical bars the standard errors. See methods for further details.



Astrocaryum
Dipteryx
Gap crown zone
n=16
Gap crown zone
n=10
Gap bole zone
n=16
Gap bole zone
n=10
Beneath adult tree
n=16
Beneath adult tree
n=10
Farther from adult
n=16
Farther from adult
n=10
Time (weeks)

Figure 4. Survival functions for seeds in the gap experiment 1, in which I investigated *Astrocaryum* and *Dipteryx* seeds survival in relation to four treatments (seeds placed in the (1) crown and (2) bole zones within gaps and seeds placed (3) beneath and (4) farther from focal adult trees located in the continuous understory). The ordinates represent the proportion of the initial population of seeds that was still alive at the start of each weekly census interval. Toe two graphs show the survival function curves for *Astrocaryum* seeds in sixteen gaps *andDipteryx* seeds in each of the ten gaps.

Astrocaryum seed survival did not differ between the four treatments. Initial seed survival of *Astrocaryum* seeds survival was different between the four treatments ("Wilcoxon test", X^2 =9.8, DF=3, p=0.020). Differences between treatments in late seed survival were not significantly different ("Log Rank test", x2 = 3.8, DF=3, p=0.287.

Dipteryx seed survival was significantly different between the four treatments. Initial seed survival was highly different between treatments ("Wilcoxon test", X^2 = 22.5, DF=3, p= 0.00005). Differences between experimental treatments on làte seed survival were also highly significant ("Log Rank test", x2 =19.1, DF=3, p=0.0002).

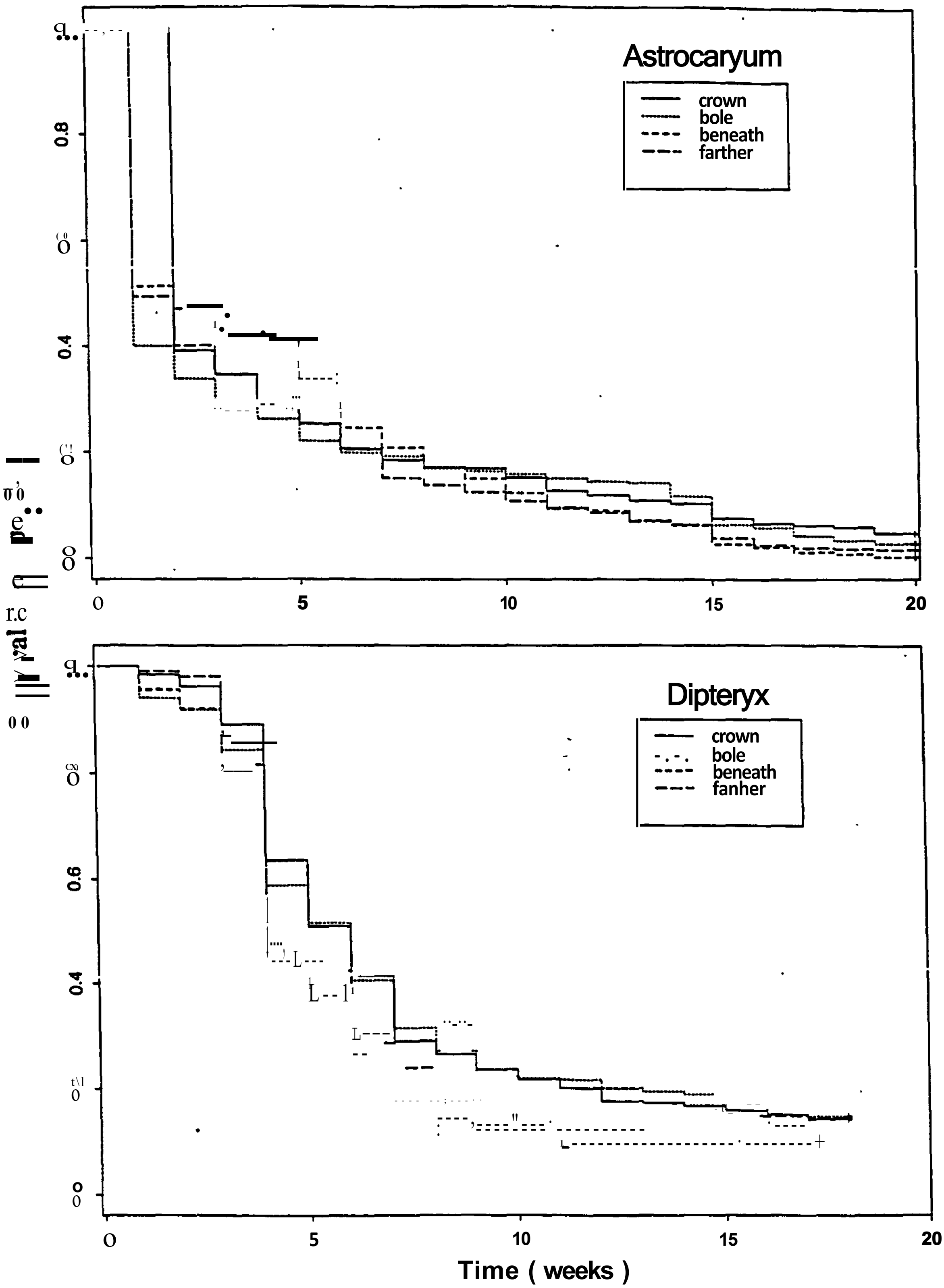
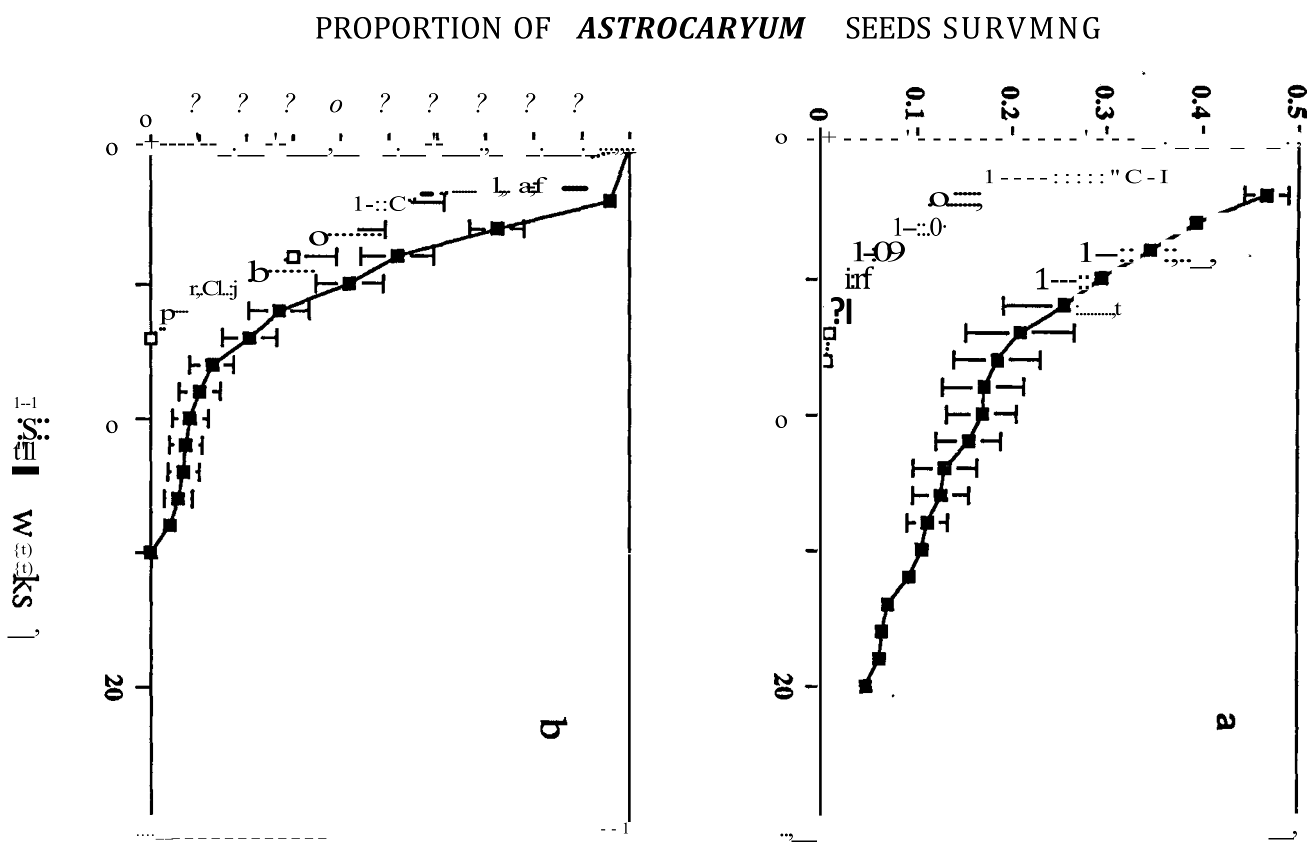

Astrocaryum
crown
bole
beneath
farther
0.8
0.4
0
5
10
15
20
Dipteryx
crown
bole
beneath
fanher
0.6
0.4
0
5
10
15
20
Time (weeks)

Figure 5. a) Fraction of *Astrocaryum* experimental seeds surviving in the understory near gaps (20-30 m) (solid squares) and far from gaps (>lO0m) (empty squares); b) Fraction of naturally occurring seeds surviving in the understory near gaps (20-30 m) (solid squares) and under trees located far from gaps (> 100 m) (empty squares).



PROPORTION OF ASTROCARYUM SEEDS SURVMNG
0
0.1
0.2
0.3
0.4
0.5
20
a
b

Figure 6. Survival function for *Astrocaryum* experimental seeds in the experiment 2, in which I investigated *Astrocaryum* seed survival in relation to two gap distance treatments: (1) seeds placed on the ground beneath adult trees located near and (2) seeds placed on the ground beneath adult trees located far from gaps. The ordinate is the proportion of the initial population of seeds that was still alive at the start of each weekly census interval. See methods for further details.

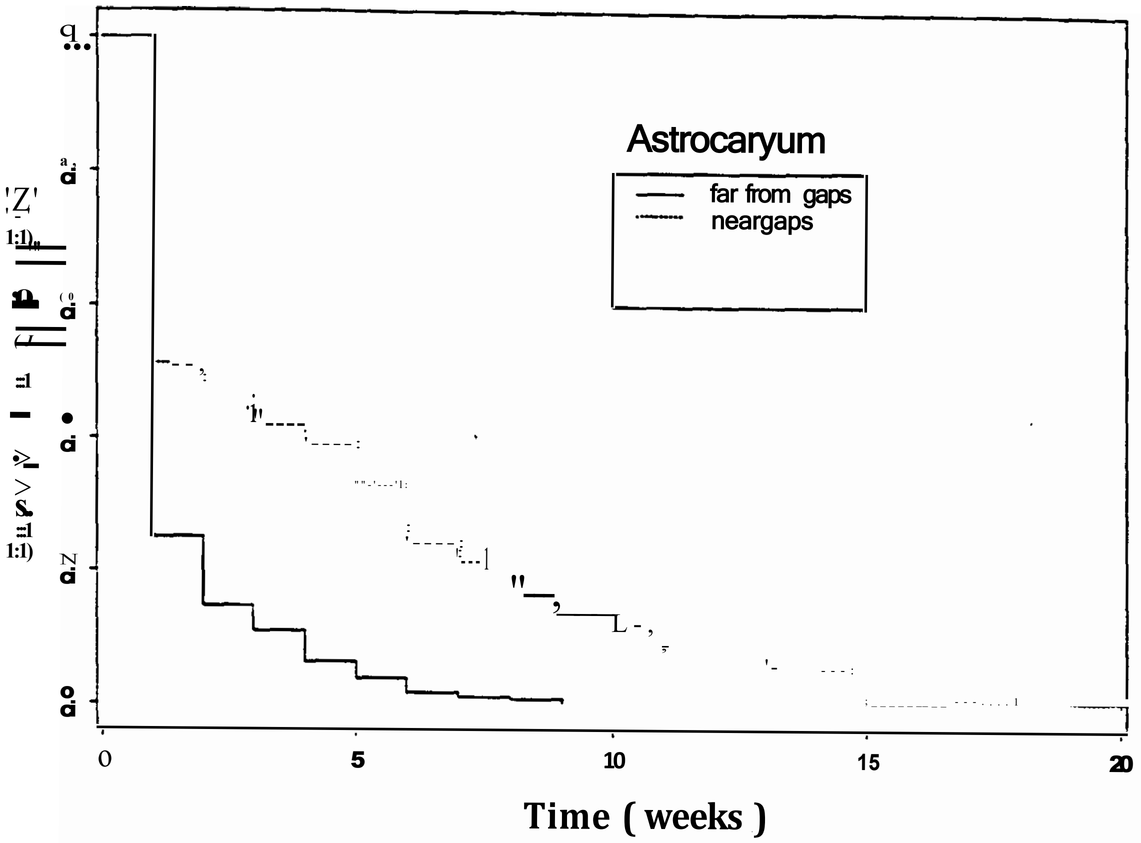
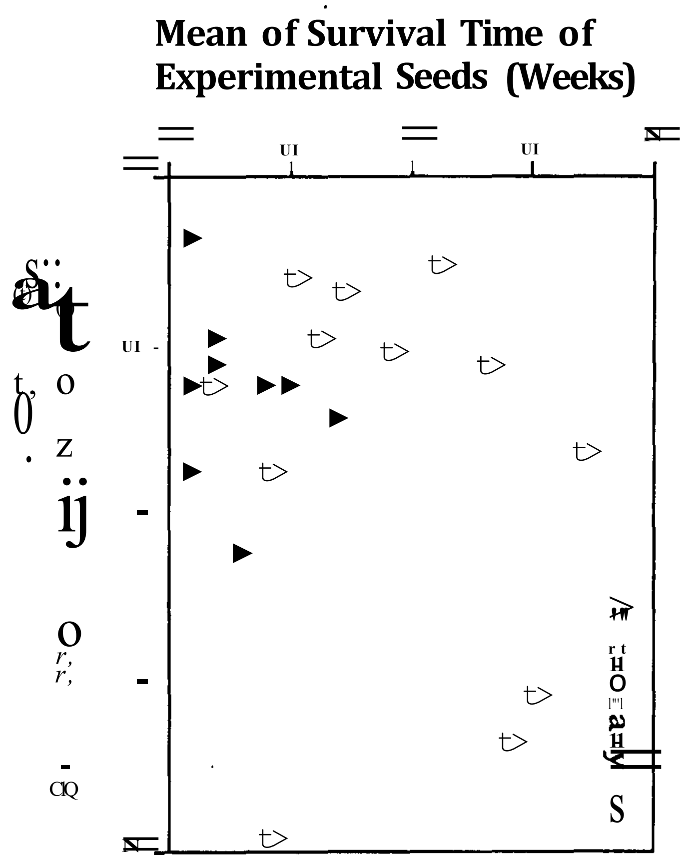

Astrocaryum
far from gaps
neargaps
0
5
10
15
20
Time (weeks)

Figure 7. Relationship between the number of weeks ***Astrocaryum*** seeds survived in groups of experimental seeds (NWEKSUV) and in the naturally occuring seed density (NATDENS) under adult trees located near (20-30m) gaps (empty triangles) and under adult trees located far (> 100m) from gaps (solid triangles).


Mean of Survival Time of
Experimental Seeds (Weeks)

Appendix 1

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