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REGENERAÇÃO NATURAL E CRESCIMENTO DE INDIVÍDUOS NÃO REPRODUTIVOS DE *Enterolobium glaziovii* BENTHAM (MIMOSACEAE).

Flavio Nunes Ramos

Flavio Antônio Maës dos Santos
Orientador

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BANCA EXAMINADORA:

Prof. Dr: FLÁVIO ANTONIO MÄES DOS SANTOS (Orientador) Flavio

Prof. Dr. ALEXANDRE ADALARDO DE OLIVEIRA Alexandre Adalardo de Oliveira

Prof. Dr. MARCELO TRINDADE NASCIMENTO

Profa. Dra. GISLENE MARIA DA SILVA GANADE

Dedico esta tese aos meus pais, Flávio Antônio Dias Ramos e Angela Maria Nunes Ramos, pois a eles devo tudo o que sou, o que fui e o que serei. Dedico-a também para o meu recém falecido avô, Orlando Manjon Ramos, um exemplo de vida, em vida. Da vida.

ÍNDICE

RESUMO GERAL

O objetivo deste estudo foi conhecer a regeneração das plântulas e jovens de *Enterolobium glaziovii* ao redor dos adultos. Esta espécie é uma árvore de dossel, descídua, e os seus adultos apresentam baixa densidade. Esse estudo foi realizado no estado do Rio de Janeiro, Brasil, em quatro parcelas circulares com 30 m de raio, tendo um indivíduo reprodutivo de *E. glaziovii* no centro de cada uma. Em todas as parcelas, valores de cobertura de dossel e graus de declividade, a chuva de frutos de *E. glaziovii*, o recrutamento de novos indivíduos, o padrão espacial, o crescimento e a sobrevivência de jovens coespecíficos, foram estimados anualmente de 1996 a 1999. Houve diferenças na topografia em cada parcela, apesar de todas as parcelas estarem em terreno inclinado. Os indivíduos jovens de *E. glaziovii* se encontravam sob alta cobertura de dossel (> 80%). O tamanho e a arquitetura da copa das plantas parentais e a inclinação do terreno influenciam a distribuição espacial dos frutos e jovens de *E. glaziovii.* O crescimento dos jovens de *E. glaziovii* é afetado negativamente pela densidade de coespecíficos, enquanto que o efeito da planta parental parece não ser importante. As plântulas desta espécie são capazes de sobreviver e crescer em uma grande amplitude de sombreamento por pelo menos 6 meses, mas apresentam maior incremento de altura em ambientes com mais de 80% de cobertura. *E. glaziovii* apresenta características de espécie tolerante a sombra. Essa espécie é capaz de geminar, se estabelecer, crescer e sobreviver em ambientes pouco iluminados. A taxa anual de mortalidade de indivíduos pequenos foi significativamente maior do que as taxas dos indivíduos médios e grandes. Não houve diferença entre o número de recrutamento observado e esperado tanto embaixo e fora da copa da planta parental, como em parcelas com alta e baixa densidade de frutos coespecíficos. A taxa de mortalidade não foi afetada embaixo da copa da planta parental nem em parcelas com alta densidade de jovens.

Portanto, os resultados parecem indicar que os processos ocorrendo na escala espacial e temporal deste estudo não explicam a baixa densidade de adultos de *E. glaziovii*. Provavelmente, os processos que promovem o esparso padrão espacial dos adultos devem ocorrer em uma maior escala espacial e / ou temporal.

Palavras chave: cobertura de dossel, crescimento, distribuição espacial de frutos, *Enterolobium*, Mimosaceae, recrutamento, taxa de mortalidade, tolerância a sombra, topografia.

GENERAL ABSTRACT

The purpose of this study was to know how was the regeneration pattern of *Enterolobium glaziovii* offspring around reproductive ones. This is a canopy and deciduous species and its adults present low density. The study was carried out in four circular plots of 30 m of radius, centered by a reproductive tree of *E. glaziovii* in Rio de Janeiro State, Brazil. From all the plots the following estimates were made: canopy coverage values and the declivity degrees, as well as the *E. glaziovii* seed shadow, recruitment of new individuals, its spatial pattern, its growth, and the survival of its offspring, were estimated yearly from 1996 to 1999. Although all the studied plots were situated on slope areas, there were differences in topography in each plot. *E. glaziovii* offspring were under high canopy coverage values (> 80%). The size and architecture of the parental crown and the slope influence the spatial pattern of *E. glaziovii* fruit and offspring. Its growth is negatively affected by conspecific density, while the parental effect is not important to it. Seedlings of this species are capable of survive and grow in a broad range of shade levels, at least for 6 months, but they present greater height increments at environments of >80% of shade. *E. glaziovii* presents several characteristics of a shade-tolerant, "non-gap" species. It is capable to germinate, establish, growth and survive in a low light environment. Small individuals presented higher annual mortality rate than medium and large ones. There was no significant difference between the recruitment number expect and observed both under and outside of the parental crown and in plots with high and low density of conspecific fruit. The annual mortality rate of offspring was not affected either by offspring density or under parental crown. Therefore, It seems that the processes occurring at spatial and temporal scale of this study do not explain the low density of the *E. glaziovii* adults. Probably, the processes that explain the sparse spatial pattern of its adults might be occurring in a larger spatial and / or temporal scale.

Keywords: canopy coverage, density-dependence mortality, *Enterolobium*, fruit spatial distribution, growth, Mimosaceae, recruitment shade tolerance, size-dependent mortality, topography heterogeneity.

INTRODUÇÃO GERAL

A luz é um importante fator que afeta a composição de espécies, o crescimento e a distribuição de plantas em florestas tropicais (Smith *et al.* 1992). Vários estudos têm revelado que os regimes de luz em florestas tropicais são espacial e temporalmente heterogêneos (Liberman *et al.* 1995, Tang *et al.* 1999). O conhecimento das variações espaciais e temporais da luz que alcança o sub-bosque é essencial para a compreensão da biologia das plantas florestais (Smith *et al.* 1992). Portanto, dados sobre luminosidade ajudam a explicar a variabilidade horizontal e vertical em florestas tropicais, tanto em termos de estrutura da vegetação quanto em composição de espécies (Hubbell & Foster 1983; Terborgh 1985).

O padrão espacial e a disponibilidade de luz dentro de florestas podem influenciar nos padrões de regeneração de espécies arbóreas (Nicotra *et al.* 1999). Porém, apesar de sua importância, há pouca informação sobre a distribuição espacial da luz que alcança o sub-bosque (Lieberman *et al.* 1995; Nicotra *et al.* 1999) e sobre a influência de espécies arbóreas de dossel nessa distribuição (Kabakoff & Chazdon 1996). Sítios com dominância de determinadas espécies arbóreas de dossel, por exemplo, podem apresentar influência no processo sucessional, afetando a composição de plantas no sub-bosque devido à influência na distribuição de luz exercia por suas copas (Guariguata *et al.* 1997).

Por outro lado, a distribuição espacial de plantas dentro de uma população é primariamente determinada pela distribuição de sementes durante sua dispersão (Clark & Clark 1984). A probabilidade das sementes caírem longe da planta mãe é dependente do seu tamanho ou do seu peso. Geralmente, um grande numero de sementes cai perto da planta parental (Forget 1992; Herrera *et. al.* 1994), principalmente as espécies que possuem sementes grandes (Richard 1996). A distribuição espacial das sementes após a dispersão é importante porque o crescimento e a sobrevivência das plantas dependem do local em que as sementes caíram (Schupp 1988). A dispersão secundaria e a mortalidade das sementes e plântulas podem alterar a distribuição inicial das sementes, afetando assim a distribuição espacial dos estádios de vida posteriores (Loiselle *et al.* 1996, Wada & Ribbens 1997).

Apesar de sementes de várias árvores das florestas tropicais serem capazes de germinar no sub-bosque (Garwood 1983), freqüentemente o crescimento e a taxa de sobrevivência das plântulas e jovens são pequenos, a menos que eles ocorram próximos ou dentro de clareiras (Augspurger 1984). As poucas plântulas que sobrevivem no sub-bosque são muito importantes na dinâmica florestal, porque as plântulas e jovens das espécies que ficam dormentes ou com o crescimento suprimido são os principais componentes de uma clareira assim que ela é criada (Brokaw 1985). Portanto, o conhecimento sobre a relação entre as condições luminosas e o crescimento de árvores pode ser utilizado em programas de produção de madeira em florestas manejadas (Webb 1999).

O padrão espacial das populações de plantas pode ser dependente tanto da densidade de sementes e plântulas, quanto da distância da planta parental (Janzen 1970). Segundo Janzen (1970) e Connell (1971), a grande concentração de sementes sob a copa da planta mãe provocaria um aumento na ação de predadores de sementes e herbívoros nesses locais, reduzindo o estabelecimento de novos indivíduos próximos a seus parentais, resultando em populações menos agregadas. Por outro lado, de acordo com Armesto *et al.* (1986), 75 - 100% das espécies de árvores tropicais apresentam padrão espacial agregado.

Segundo Leite & Hay (1989), o estudo da regeneração natural de espécies florestais nativas é de fundamental importância, como parte integrante do conhecimento da biologia reprodutiva dessas espécies e para auxiliar na resposta a muitas questões sobre o manejo dessas espécies. Porém, apesar da importância de tal estudo, o conhecimento sobre a regeneração natural de espécies nativas em florestas é escasso ou insatisfatório. Por esta razão, há a necessidade urgente de estudos sobre o processo de regeneração de espécies arbóreas brasileiras, pois este tipo de estudo fornecerá subsídios para um melhor entendimento da dinâmica dessas espécies, assim como poderá contribuir de modo significativo para o manejo das mesmas.

OBJETIVO GERAL

Nesta tese foram estudados alguns aspectos da regeneração de *Enterolobium glaziovii* e alguns de seus fatores. As questões a serem respondidas foram: (1) há variação espacial e temporal na cobertura de dossel e na topografia ao redor de adultos reprodutivos de *E. glaziovii*? (2) o tamanho e a arquitetura da copa da planta parental influencia a distribuição espacial dos frutos e jovens de *E. glaziovii*? (3) O crescimento de jovens de *E. glaziovii* é afetado embaixo da copa do adulto parental e pela densidade de jovens coespecíficos? (4) o recrutamento das plântulas e a mortalidade dos jovens de *E. glaziovii* são afetados embaixo da copa da planta parental e pela densidade de frutos e jovens coespecíficos?

Cada uma dessas quatro questões foi abordada em um capítulo desta tese com o objetivo de conhecer a regeneração de *Enterolobium glaziovii*, assim como alguns dos seus aspectos mais críticos e importantes. Os autores de cada um dos capítulos foram Flavio Nunes Ramos, Dalva Maria Silva Mattos e Flavio Antônio Maës dos Santos.

A tese foi desenvolvida dentro de parcelas circulares de 30 m de raio, centralizadas em um adulto de *Enterolobium glaziovii*. Apesar dos jovens terem sido estimados dentro de todas as parcelas, os frutos foram apenas amostrados dentro das mesmas por 4 setores de 5 graus com 30 m de extenção, partindo da adulto central até o final as parcelas (figura 1)

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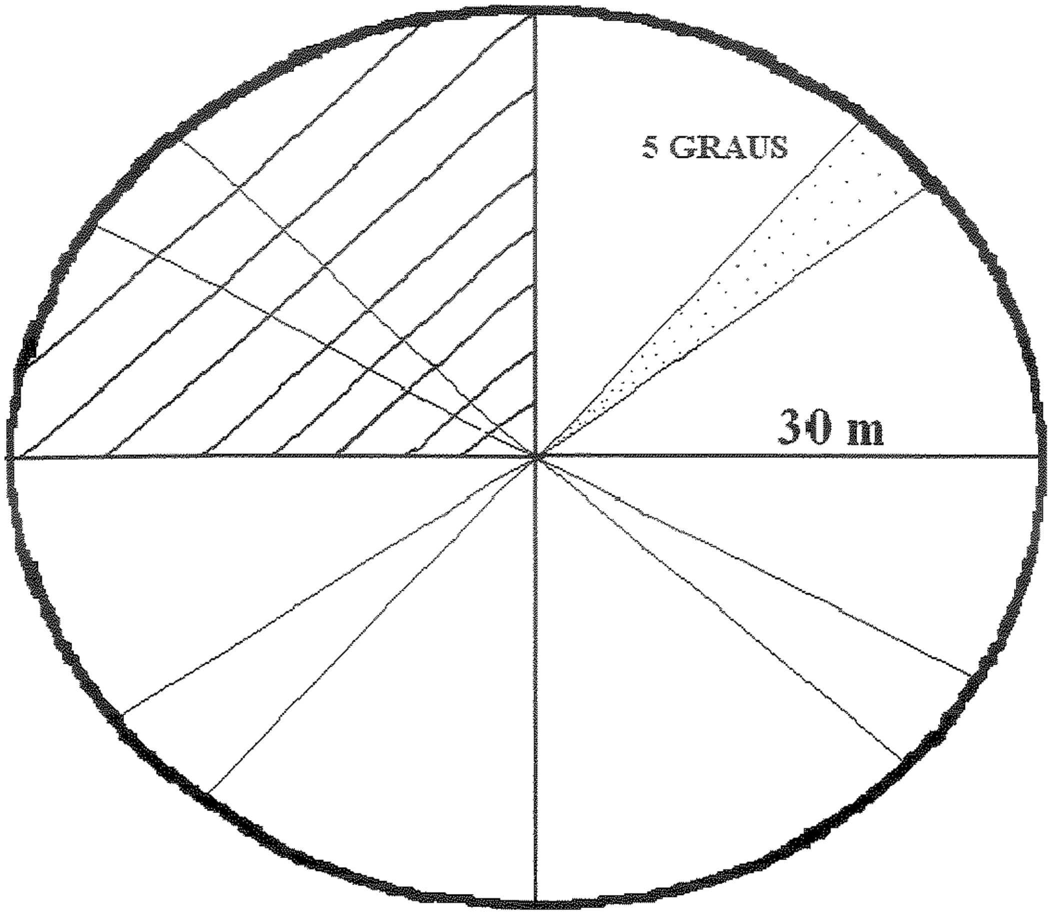

Figura 1: Esquema de uma parcela circular com 30 m de raio, centralizada em um adulto de *Enterolobium glaziovii*, utilizada nesta tese. A área rachurada representa uma das quatro sub-parcelas onde os jovens de *E. glaziovii* foram estimados, e a área pontilhada representa um dos quatro setores de 5 graus nos quais os frutos da mesma espécie foram amostrados.

CAPÍTULO 1

CANOPY COVERAGE AND TOPOGRAPHY HETEROGENEITY AROUND REPRODUCTIVE TREES OF *Enterolobium glaziovii* BENTHAM (MIMOSACEAE)[1]

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[1]- Nos moldes da revista Journal of Vegetation Science.

Resumo

A luz e a topografia são fatores importantes que afetam a composição de espécies, o crescimento e a distribuição de plantas em florestas tropicais. Este estudo foi realizado em quatro parcelas circulares com 30 m de raio, ao redor de árvores reprodutivas de *Enterolobium glaziovii* no estado do Rio de Janeiro (22°29'-22°58'S, 42°13'-43°13'W), SE Brasil. Foi considerado que amostras ao redor de uma única espécie arbórea reduz a variabilidade gerada pelas diferentes características das copas de diferentes espécies, permitindo comparações de heterogeneidade da cobertura do dossel entre parcelas. O objetivo deste trabalho foi responder às seguintes questões: (1) Existem diferenças espaciais e sazonais na cobertura de dossel em torno de árvores de *E. glaziovii*? (2) Existem diferenças entre os valores de cobertura de dossel medidos em duas alturas diferentes (na altura do solo e do peito, 1,3 m)? (3) Existem variações topográficas dentro e entre parcelas? Os valores de cobertura do dossel foram estimados à 1,30 m (altura do peito) e na altura do solo, a cada três meses durante 1998, em cada parcela. A estrutura da vegetação de cada parcela, número de árvores, área basal total e alturas de indivíduos acima de 10 cm de diâmetro à altura do peito foi descrita, com o objetivo de verificar possíveis relações com as variações de cobertura do dossel dentro e entre parcelas. A declividade em cada parcela foi medida com clinômetro. Três parcelas apresentaram altos (> 80%) valores de cobertura de dossel sem diferenças espaciais entre as alturas de medida. Apenas em uma delas houve variação espacial, com valores altos (> 80%) de cobertura de dossel embaixo da copa do indivíduo central e valores altamente variáveis fora da copa, na altura do peito. Não houve diferenças sazonais nos valores de cobertura de dossel. Apesar de todas as parcelas estarem em terrenos inclinados existiram diferenças na topografia dentro de cada parcela. A variação espacial nos valores de cobertura de dossel encontrados em uma das parcelas (B2) provavelmente ocorre devido à estrutura da vegetação nessa parcela, que apresentou poucas árvores grossas, e árvores mais baixas afastadas (20 a 30 m) do que as mais próximas do indivíduo central. Essa estrutura da vegetação na parcela, com árvores finas e esparsas, torna freqüente a presença de clareiras pela descontinuidade das copas dessas árvores no dossel, provocando variações nos valores de cobertura de dossel nesta parcela. Portanto, na escala deste estudo, a cobertura de dossel ao redor de adultos de *E. glaziovii* em áreas florestais não perturbadas é homogênea no espaço e no tempo e a topografia espacialmente heterogênea.

Abstract

The purpose of this study was to verify the spatial and seasonal differences in canopy coverage around reproductive trees of *Enterolobium glaziovii,* as well as, the topographic variations. The study was carried out in four circular plots with 30 m of radius centered on a reproductive tree of *E. glaziovii* in Rio de Janeiro State (22°29’-22°58’S, 42°13’-43°13’W), SE Brazil. Canopy coverage values were estimated at 1.30 m (breast height) and ground heights, at every three months during 1998, in each plot. The structure of the vegetation of each plot (number of trees, basal area and height) was described, in order to relate it with possible canopy coverage variations inside and among plots. Declivity was taken in each plot. Three plots presented high (>80%) canopy coverage values, and there was no spatial difference between the height measures. Only in one of them (B2), there were spatial differences, where the canopy coverage values under *E. glaziovii* central crown were high, and out of it, at breast height, highly variable. There were no seasonal differences among the plots. Although all the plots studied were at slope areas, there were differences in topography within each one. Spatial differences in canopy coverage values found in B2, was probably due to the structure of the vegetation of this plot that presented few thicker trees, and the trees out of *E. glaziovii* adults were shorter than the near ones. Furthermore, there were many gaps, which is responsible to the high variation of canopy coverage values. Therefore, in the study scale, the canopy coverage values around *E. glaziovii* adults in undisturbed forest sites are spatially and seasonal homogeneous and the topography is spatially heterogeneous.

Keywords: Atlantic forest, Brazil, canopy coverage, ombrophilous dense forest, Rio de Janeiro, seasonal variation, topography.

Introduction

Spatial and temporal environmental heterogeneity influence both the dynamics and structure of ecological communities (Vivian-Smith 1997). Spatial heterogeneity of environmental traits promotes heterogeneous distributions of the organisms and, in turn, affects the performance and fate of individuals at the local environment (Nunez-Farfan & Dirzo 1988). In its turn, topography (Basnet 1992) and light (Smith *et al.* 1992) are important factors, which affect the composition of species, growth and distribution of plants in tropical forests. Topographical features are important physical factors, which create diverse microsites depending upon the soil type, moisture regimes, geological formation and altitude (Basnet 1992; Vivian-Smith 1997).

Most of the studies on distribution of tree species have been related to large-scale topographical variations, while the small-scale distribution of individual species rarely has been investigated. However, local topographic variations promote the patches of microhabitats, which maintain the complexity and diversity of an ecosystem (Basnet 1992). Explanation for such patterns includes differential seed accumulation, variation in species germination requirements and differences in growth and mortality at different microtopographic positions (Vivian-Smith 1997).

On the other hand, many studies have revealed that light regimes in tropical forests are spatially and temporally heterogeneous (Liberman *et al.* 1995; Tang *et al.* 1999). Knowledge of spatial and temporal variations in the understory light environment is essential for an understanding of forest plant biology (Smith *et al.* 1992).

Most studies of light regime in tropical forest focused on the difference between the gaps and the understory, or among gaps of various sizes (Denslow 1980, 1987; Bellingham *et al.* 1996; Tang *et al.* 1999). But there are studies that focused at a landscape level, such as the effects of hurricanes on forest light regimes (*e.g.* Bellingham *et al.* 1996). Other studies measured variations on light regimes at smaller spatial scales, such as that of individual leaves or seedlings within a gap or within the understory (Tang *et al.* 1999). Because light is considered a major factor limiting growth and survival of many forest species, the spatial pattern of light availability within forest stand are likely to influence stand-level regeneration patterns of woody species (Nicotra *et al.* 1999). In spite of its importance there is little information on the distribution of understory light availability (Lieberman *et al.* 1995; Nicotra *et al.* 1999) and little information about the influence of the canopy species on this distribution (Kabakoff & Chazdon 1996). Site specific dominance by canopy individuals may further influence sucessional trajectories by creating distinct light environments, and potentially affecting plant composition in the understory (Guariguata *et al.* 1997). The extent to which different canopy dominants may influence vegetation dynamics in the understory is a topic that deserves further investigation in tropical secondary forests (Kabakoff & Chazdon 1996).

This study was performed in four plots around reproductive trees of *Enterolobium glaziovii*. We consider that samples around individuals of single species reduce the variability generated by different crown characteristic of different species, and thus, enable us to compare the canopy coverage heterogeneity among plots. The purpose of this study was to answer the follow questions: (1) are there spatial and seasonal differences in canopy coverage in the plots? (2) Are there differences between the canopy coverage values measured by two different height measures (ground level and breast height, 1.3m) inside the plots? (3) Are there topographic variations inside and among plots?

To answer these questions we compared the canopy coverage variation on two heights and the topographic variation, in each plot. We predicted that (1) The canopy coverage values under the central *E. glaziovii* crown would be spatially and seasonally less variable than out it, because out it there are many different tree species with different crown size and shapes generating higher heterogeneity. (2) The canopy coverage values on ground level would be higher than on breast height, due to the inclusion of other crown of small plants and shrubs. (3) The canopy coverage values on breast heights would be more seasonal variable than on ground height due to the fact that, in general, there are more subcanopy and canopy species that are deciduous than shrubs and understory ones (Morellato 1991).

Methods

Study area

The study was carried out in four circular plots with 30 m of radius centered on a reproductive tree of *E. glaziovii*. Three of them (B1, B2 and B3) were in the Biological Reserve of Poço das Antas (BIORE) (22°29' - 22°36'S, 42°13' - 42°21'W) and one of them (R1) in the National Park of Tijuca, near the Rio de Janeiro Botanical Garden (RJBG) (22°58'S, 43°13'W) in Rio de Janeiro State, Brazil. Both areas are at evergreen forest, or Ombrophilous Dense Forest (*sensu* Velloso *et al.* 1991). At the BIORE, the mean annual temperature is 27.6°C in summer and 21.3°C in winter, and the mean annual rainfall is 2091.9 mm (IBDF 1981b and data from the Golden Lion Tamarin Association obtained from 1983 to 1998). At the RJBG, the mean annual temperature is 29°C in summer and 22°C in winter, and the mean annual rainfall is 1075 mm (IBDF 1981a; Coelho Neto 1985 *apud* Oliveira & Lacerda 1988). All the reproductive trees that were found, were sampled and were isolated and very far from one another. The four plots were very distant from each other, from 126 km between the BIORE and the RJBG to 2.5 - 10 km among the BIORE trees.

Among the plots, only B2 suffered antropic perturbation. It is located inside abandoned grassland. The *E. glaziovii* reproductive tree and some other taller and thicker trees sampled at B2 probably are remnants of the past forest, which was cut down to form a grassland for human exploitation, before the implantation of the Biological Reserve. On the other hand, R1, B1 and B2 were at forest sites that did not suffer this kind of perturbation (IBAMA pers. comm.).

Study species

Enterolobium (Mimosaceae) is a neotropical genus distributed from Central America (Mexico) to South America (Argentina) with Amazon as it center of diversity (Mesquita 1990). Timber of this genus is used to make boats, packing cases and scantlings. The species are separated mainly by fruit morphology, which are predominantly indehiscent. Among of the 10 species of the genus, *E. glaziovii* presents restrict geographic distribution, it had just been collected at three states of Brazil: Rio de Janeiro, Espirito Santo and Bahia, being endemic of the Brazilian Coastal Atlantic forests (Mesquita 1990). It occurs in low frequency at forest sites (Lima, H. C. Botanical Garden of Rio de Janeiro, Brazil, pers. comm.). It is a canopy tree, and its reproductive individuals range from 8 to 30 m tall (Mesquita 1990). The *E. glaziovii* trees lose its leaves yearly in May, while its fruit fall yearly about May and June.

Canopy coverage

Canopy coverage values were estimated at 1.30 m (breast height) and at ground heights with a spherical densiometer. Samples were taken at each 5 m, from the central *E. glaziovii* to the limit of each plot, along eight transects located at compass directions. The canopy coverage values were estimated at every three months (in the beginning of each season) during 1998. Thus, at each season, canopy coverage values were recorded at 48 points at each height, in each plot.

In order to describe and compared the structure of each plot, the number of all trees with diameter at breast height (DBH) ≥10 cm in each circular plot (2827,35 m^2 each plot) were quantified and their heights were sampled. To sample the heights of trees, at each 5 m, from the central *E. glaziovii* to the limit of each plot, along eight transects at compass directions, the height of one individual tree with DBH ≥10 cm was visually estimated in each 5 m class. Thus, the height of 48 trees was recorded, in each plot. Basal area for each individual was calculated as $\pi\ (DBH/2)^2$.

Topography

Declivity was taken at each 10 m along four transects at compass directions, from the central *E. glaziovii* to the limit of each plot, using a clinometer. Declivity values of transects on down-slope direction (areas above the central *E. glaziovii*), are considered positive and declivity values of transects on up-slope direction (areas below it), are considered negative.

Data analysis

In order to evaluate the heterogeneity, total range of measured values and its variations was considered. The distribution of canopy coverage values, the distribution of height of trees with DBH ≥10 cm, and the declivity values, in each plot, were compared by box plots. In box plots, differences among values were estimated by the overlaying of confidence interval (95%) values of the median.

Results

There were no spatial or seasonal differences in canopy coverage values (hereafter CCV) among the plots, except for one of them. Three plots (figures 1-3) presented high

CCV (>80%) and no difference between breast and ground height measures. In one plot (B2) (figure 4), there was difference between the breast and ground height measures of CCV and under (up to 10 m from its bole) and out of the central *E. glaziovii* crown. On breast height, CCV was higher (>80%) under the central *E. glaziovii* crown than out of it, where CCV presented high variation, while on ground height, CCV were high (>80%) and presented low variation (figure 3).

The structure of the vegetation of each circular plot was different. B3 plot presented the greatest number of trees and B2 presented the lowest. Moreover, R1 and B3 plots presented the greatest basal area and B2 presented the lowest (table 1). On the other hand, in a general way, the height of the trees sampled in the plots did not differ among them. However, in B1 and B2 plots, the trees near (<10 m) central adult tree were taller than far from it (figure 5).

Although all the plots studied were at slope areas, there were differences in topography among the four directions within each plot (figure 6). R1 and B2 presented more declivity variation than the other two plots. R1 presented the greatest declivity degree (60°) on down-slope direction while B2 presented the greatest (57°) on up-slope direction. Thus, R1 presented the greatest declivity degree from the central *E. glaziovii* to the edge of the circular plot, while B2 presented it from the edge of the circular plot to the central *E. glaziovii*.

Discussion

The high (>80%) CCV and its low variation found in three of the plots were probably due to the occurrence of few small gaps, and the absence of larger ones. It seems that, the number of trees and the tree basal areas found in B1, the second plot with lower values, were sufficient to promote high CCV. Because the relation between the density of thicker trees in a area influence its crown overlaying and consequently the canopy coveragge. The CCV variation found in B2 was probably related to change on the structure of this plot due to human disturbance. The difference of CCV between under and out of the *E. glaziovii* central crown observed in this plot probably occurs due to the few thicker and shorter trees out of *E. glaziovii* crown, which generate numerous relatively small and some larger canopy openings. According to Kabakoff & Chazdon (1996), current patterns of light availability may reflect historical aspects of stand development.

The similarity between the CCV at breast and ground height measures indicate that there was no difference between the light environment in which small plants or early seedlings are growing with saplings or shrubs of about 1.5 m taller. The differences between the height measures found in B2, whose ground measures presented high (>80%) CCV with low variation, and breast measure that presented lower CCV median with high variation out of central *E. glaziovii* crown, were probably due to the many grasses and short shrubs in its gaps.

The seasonal deciduousness of the *E. glaziovii* adult did not generate a decrease in CCV in the plots. The four plots are at evergreen forest where few tree species are deciduous (Richard 1996). Probably *E. glaziovii* was one of the few species in the plots, or the only one that lost its leaves. Lowman (1986) did not found seasonal variation in canopy openness for three "rain forests" (two temperate and one subtropical) in Australia. This author hypothesized that the lack of seasonal variation in canopy openness is due to the multilayered structure of the canopy. At B2, although, there were not many thicker trees, there were high (>80%) CCV under *E. glaziovii* adult crown, without seasonal variation.

Probably the crown of the several thin trees, those that were under its crown (*pers. obs.*), compensated the leave loose of *E. glaziovii* central.

In each plot there were great heterogeneity in slopes among the directions and within each direction. This kind of heterogeneity on forest ground has been suggested as an important factor for the plant species coexistence, as different species may establish preferentially on different microsites (Lusk 1995). Microtopographic variation has been strongly correlated with plant distribution and performance. Explanations for such patterns include differential seed accumulation, variation in species germination requirements and differences in growth and mortality at different microtopographic positions (Vivian-Smith 1997). Thus, the heterogeneity at small scale that was found in this study could generate aggregated patterns of seeds or diaspores, and consequently, many patches of seedlings in each plot.

Thus, the variation of light at B2, due to the presence of gaps, could create a secondary pattern of species distribution, different from the pattern generated by the topographic variations. Patches of early-germinated seeds created by topography variation that were below small gaps could present greater recruitment and growth than ones located at understory. Hence, it is expected that at B2 there is greater number of species than the other plots, as it stands with larger range of light availability should have higher woody seedling abundance and species richness (Nicotra *et al.* 1999).

Therefore, in this study scale, the canopy coverage values around *E. glaziovii* adults, in undisturbed forest sites, are homogeneous spatial and seasonally and the topography is spatially heterogeneous. High canopy coverage values (>80%) could limit the range of plant species that are able to germinate, establish and growth around *E. glaziovii* adults. Nevertheless, the topographic heterogeneity could perform a relevant influence on the spatial distribution of the seed, its germination and plant establishment of species do not limited by high CCV. Variation on topography will distribute differently the seeds, due to its morphology, to many distinct microsites. Pre-existent plant species also could influence the seedling species composition, because they will produce most of the seeds that will be dispersed, around *E. glaziovii*.

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Table 1: The number of trees ≥ 10 cm diameter at breast height and the total basal area of each plot (0.28 ha). R1 was at Parque Nacional da Tijuca, near Rio de Janeiro Botanical Garden (RJBG), and B1, B2 and B3 were at Biological Reserve of Poço das Antas (BIORE) in Rio de Janeiro State, Brazil.

	R1	**B1**	**B2**	**B3**
Number of trees	168	145	58	250
Basal area (m^2)	972.1	504.9	166.3	941.9

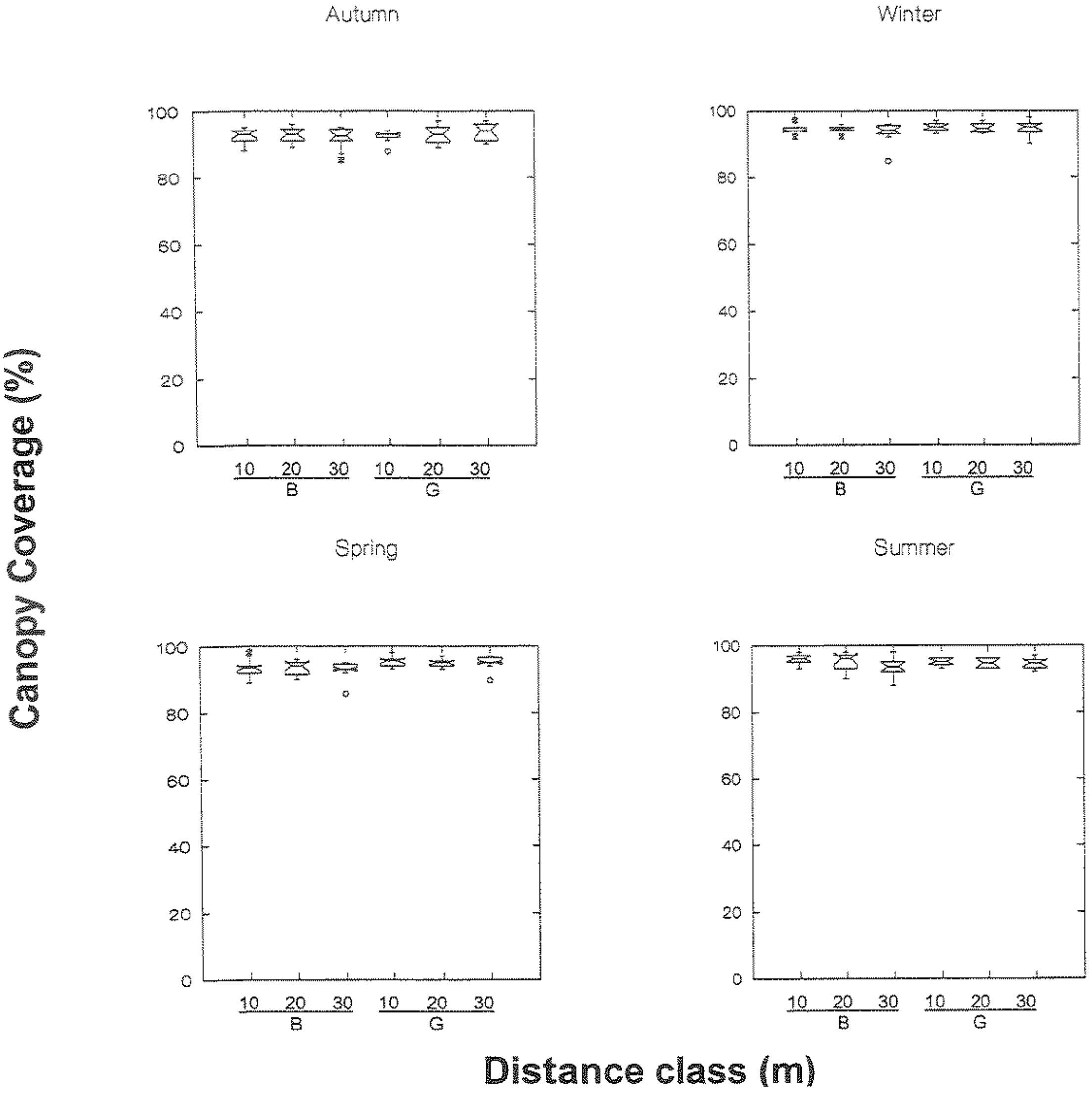

Figure 1: Canopy coverage (%) at each 10 m, at breast (B) and ground (G) height and on each season at R1. Box plot presents median (horizontal line in the box), 25th and 75th percentiles (box), and minimum and maximum values (whiskers). The asterisks mark the value outside the acceptable range, and the circles mark the values "far outside" the acceptable range. The box are notched at the median and return to full width at the lower and upper confidence interval (95%) values.

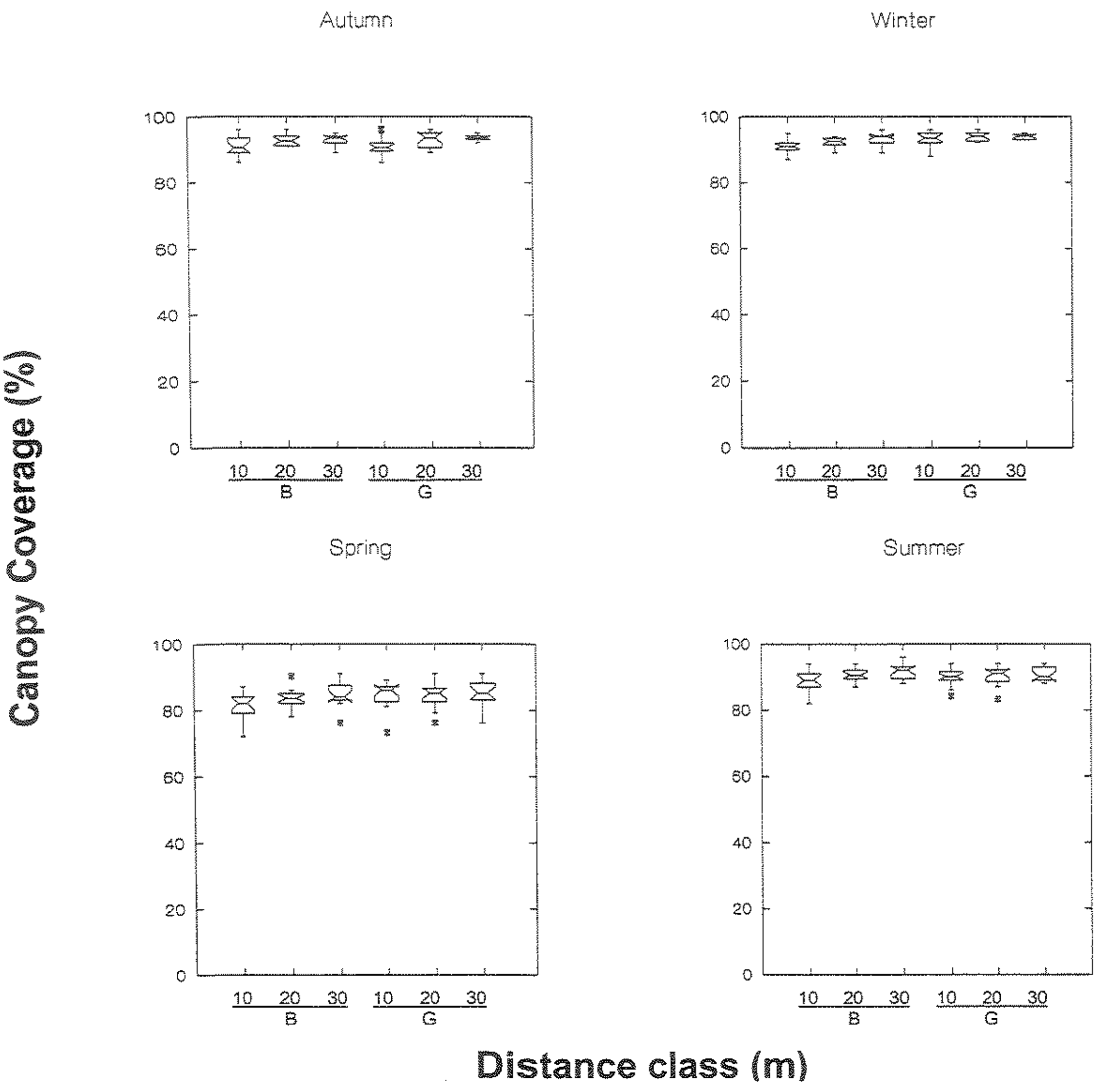

Figure 2: Canopy coverage (%) at each 10 m, at breast (B) and ground (G) height and on each season at B1. See fig 1 to Box Plot legends.

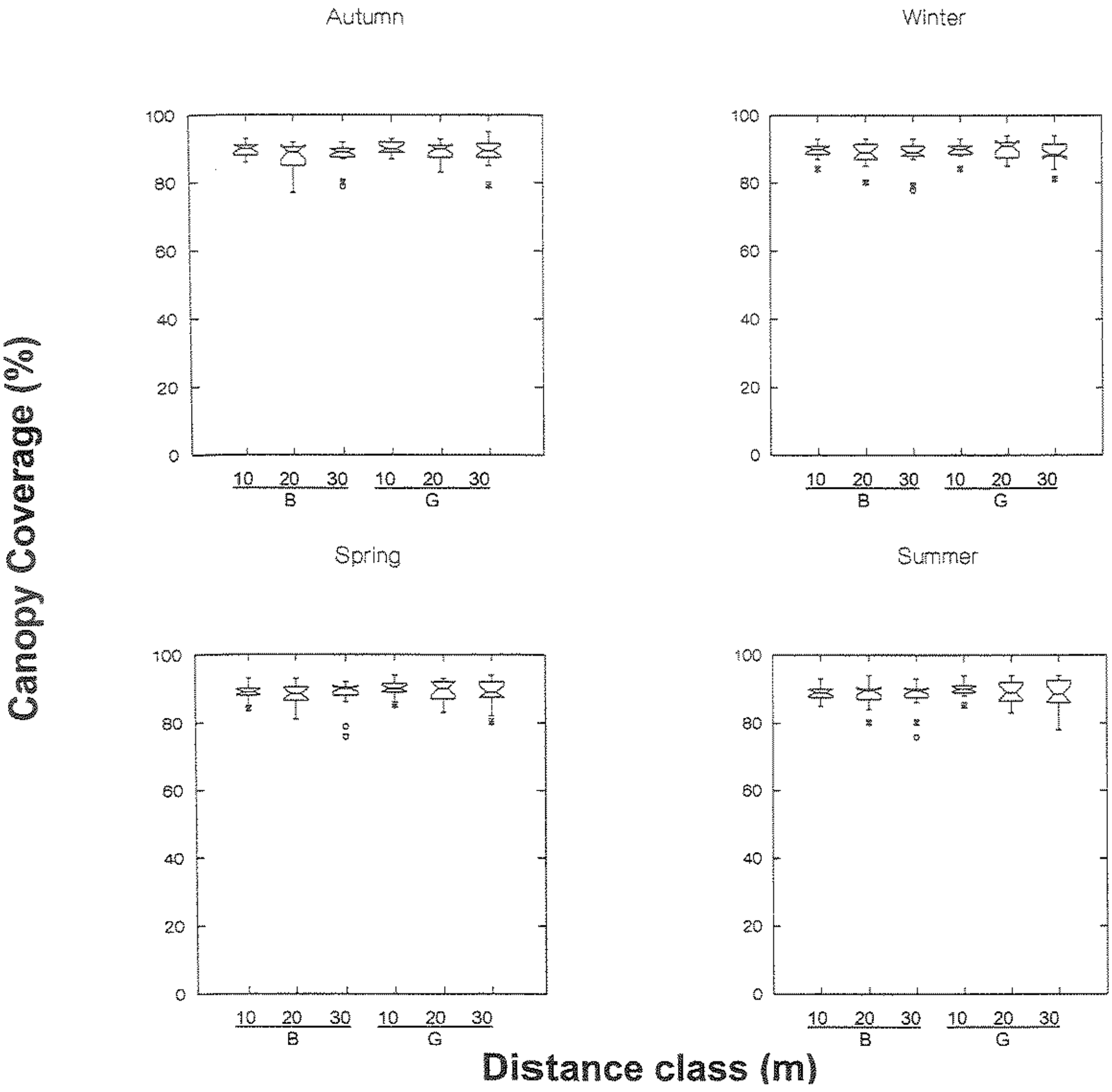

Figure 3: Canopy coverage (%) at each 10 m, at breast (B) and ground (G) height and on each season at B3. See fig 1 to Box Plot legends.

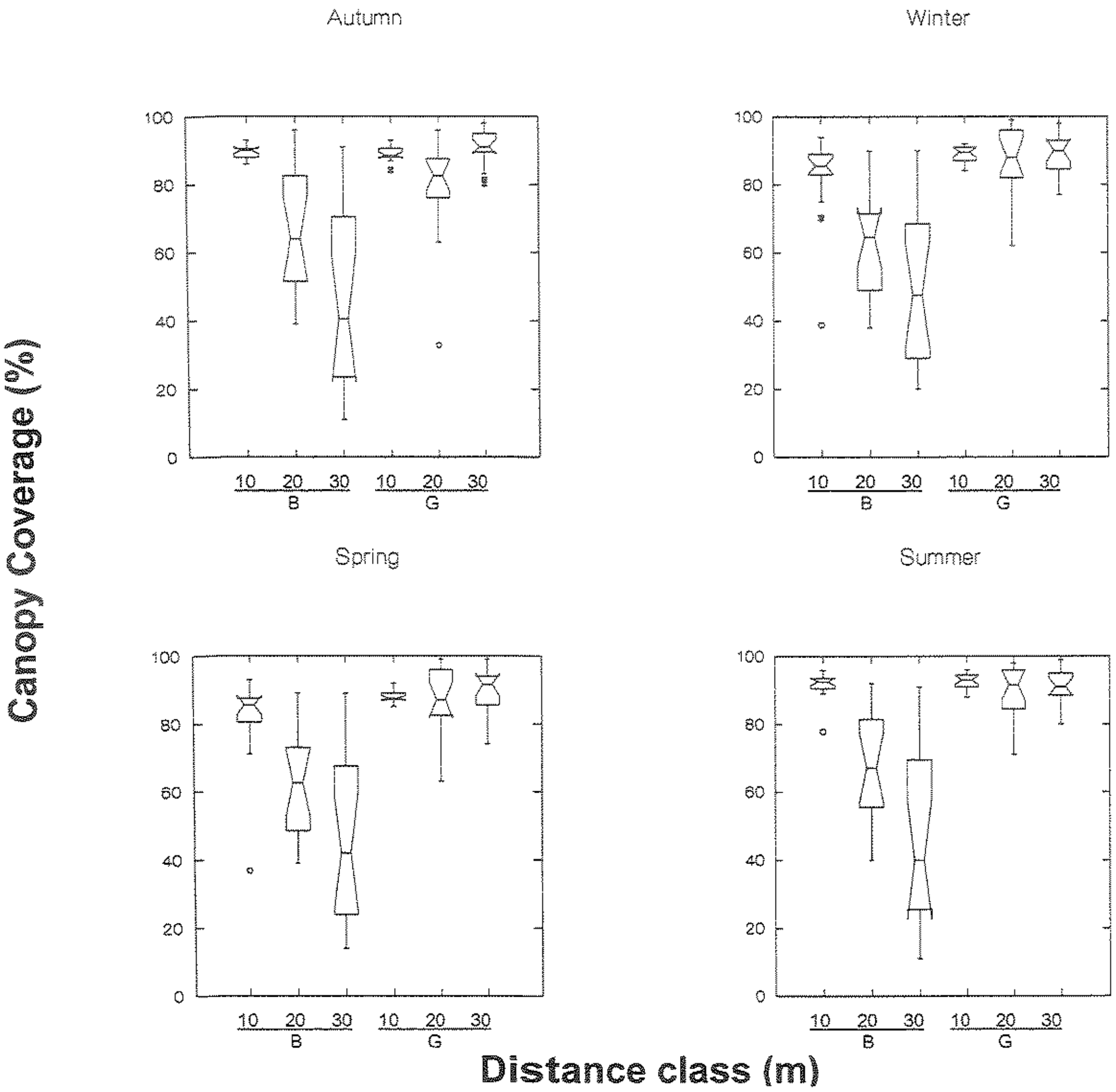

Figure 4: Canopy coverage (%) at each 10 m, at breast (B) and ground (G) height and on each season at B2. See fig 1 to Box Plot legends.

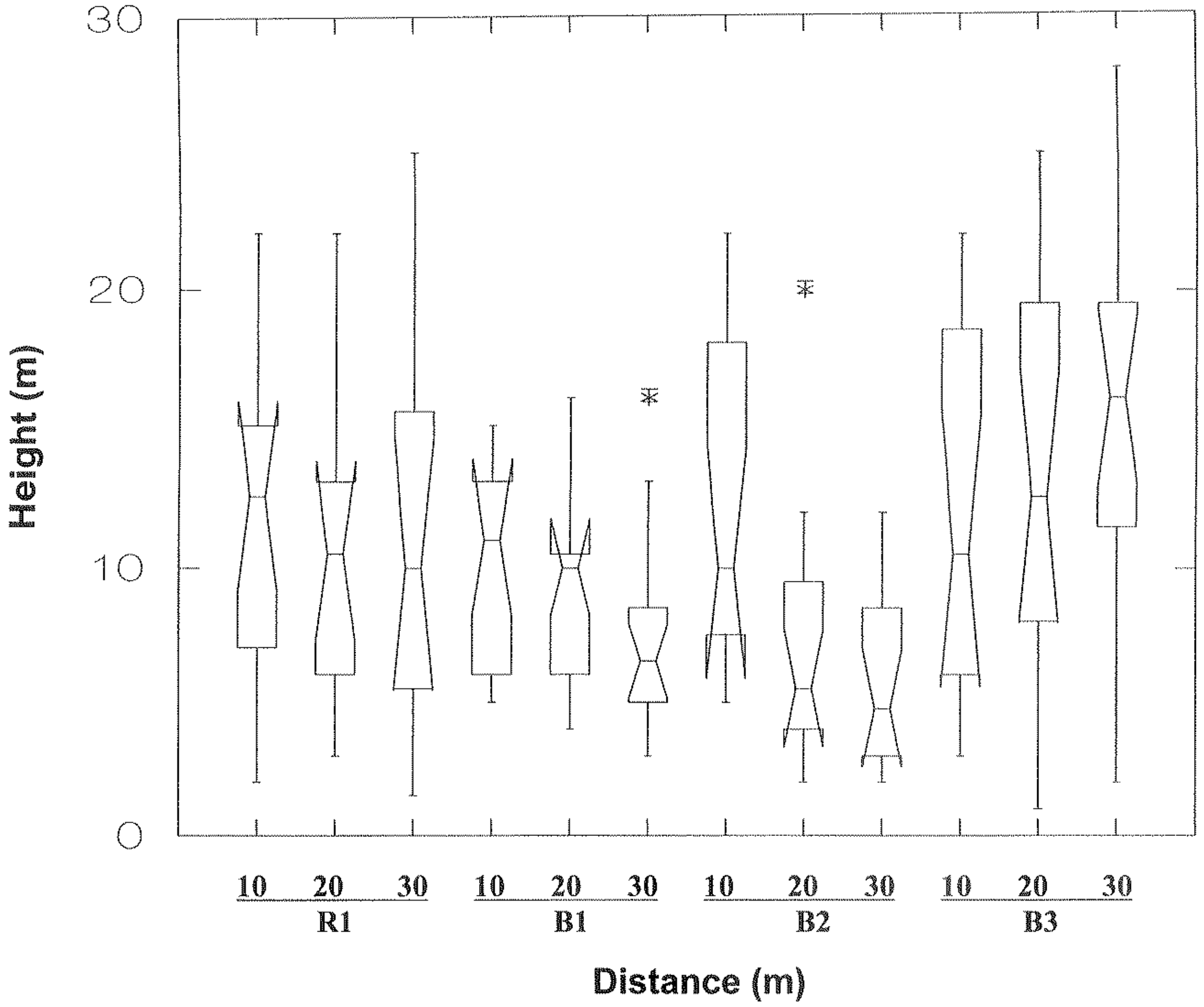

Figure 5: Height (m) of trees ≥ 10 cm DBH at each 10 m, at R1, B1, B2 and B3. See fig 1 to Box Plot legends and see table 1 to plot legend. The height of 48 trees was recorded, in each plot.

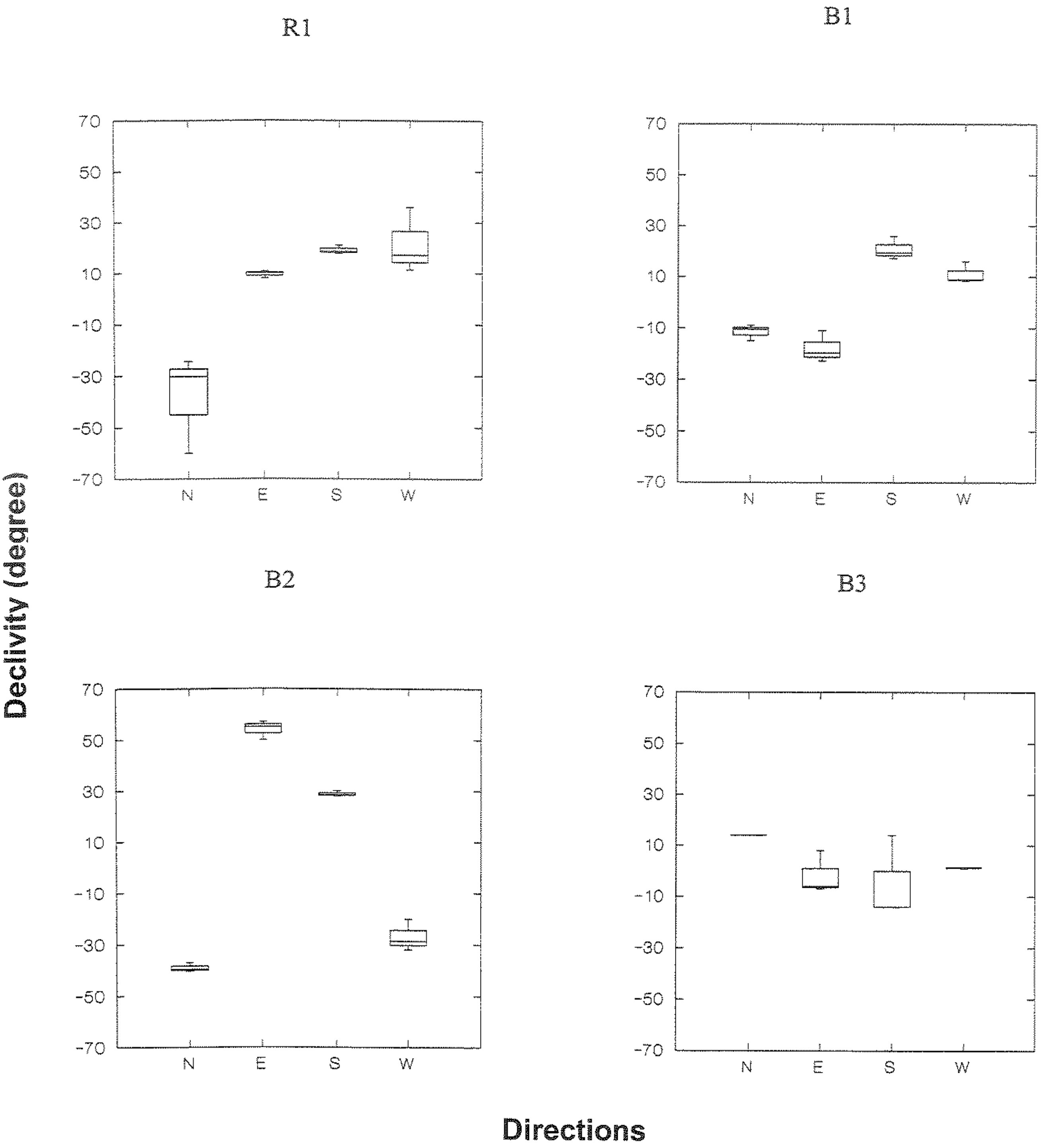

Figure 6: Declivity degree to North (N), East (E), South (S) and West (W) directions, at R1, B1, B2 and B3 plots. See fig 1 to Box Plot legends. (+) = down-slope (areas above the central *E. glaziovii*) and (-) = up-slope (areas below it).

CAPÍTULO 2

SPATIAL DISTRIBUTION OF SEEDS AND OFFSPRING OF *Enterolobium glaziovii* Bentham (MIMOSACEAE) AROUND REPRODUCTIVE TREES[1]

1 Nos moldes da revista Biotropica

ABSTRACT

The spatial pattern of *Enterolobium glaziovii* fruit and offspring was evaluated in four circular plots with 30m of radius, centered on a reproductive tree of this species to verify whether the size of the parental crowns and the topography has any influence on the spatial distribution of its fruit and offspring. The plots were in the Rio de Janeiro state (22°29'-22°58'S, 42°13'-43°13'W), SE, Brazil. Each crown was subdivided in four irregular triangles and the area (m^2) of each one was calculated. All the plots, which were in slope areas, were subdivided in four sub-plots, two of them on up-slope direction (above the central reproductive tree), and the other two sub-plots on down-slope direction (below the central reproductive tree). The numbers of fruit (in 1998 and 1999) and offspring (from 1996 to 1999) of *E. glaziovii* were registered under and out of the central reproductive tree, under each one of the crown triangles and in each topography sub-plot. Although there were more fruit under the parental crown, there was no difference in the offspring number under and out of it. There was correlation between the area of the crowns and the fruit number under it, while with the offspring number there was not. Most of the fruit and the offspring were on down-slope directions. Therefore, the size of the parental crown has influence on the spatial distribution of the *E. glaziovii* fruit, whereas the topography has influence both on spatial distribution of its fruit and offspring. These results indicate that there should be a higher probability of establishment of the *E. glaziovii* offspring out of its parental crown.

RESUMO

O padrão espacial dos frutos e jovens de *Enterolobium glaziovii* foi avaliado em quatro parcelas circulares de 30 m de raio, centralizadas em um adulto de *E. glaziovii* para verificar se o tamanho da copa da planta parental e se a topografia do terreno influenciam o padrão espacial de frutos e jovens desta espécie. As parcelas se encontram no estado do Rio de Janeiro (22°29'-22°58'S, 42°13'-43°13'W), SE, Brasil. Cada copa foi dividida em quatro triângulos irregulares e foi calculada a área (m^2) de cada um. Todas as parcelas (que estão em terrenos inclinados) foram divididas em quatro sub-parcelas, sendo duas na direção da subida do terreno (acima do adulto central de *E. glaziovii*) e duas na direção da descida do terreno (abaixo do adulto central). Os números de frutos (em 1998 e 1999) e jovens (de 1996 a 1999) foram avaliados embaixo e fora da copa, embaixo de cada um dos triângulos de copa, e dentro de cada sub-parcela da topografia. Apesar da maioria dos frutos estarem embaixo da copa da planta parental, não houve diferença significativa entre o número de jovens embaixo ou fora da copa das mesmas. Enquanto houve correlação entre o tamanho das copas e o número de frutos embaixo das mesmas, não houve correlação com o número de jovens. Além disso, a maioria dos frutos e jovens estava nas sub-parcelas de descida. Portanto, o tamanho da copa das árvores parentais exerce influência no padrão espacial dos frutos de *E. glaziovii*, enquanto a topografia exerce influência tanto no padrão espacial dos frutos como dos jovens. Os resultados indicam que deve haver uma maior probabilidade dos jovens desta espécie se estabelecerem fora das copas das árvores parentais.

Key word: Atlantic forest, Brazil, conspecific influence, *Enterolobium*, evergreen forest, fruit shadow, Mimosaceae, offspring spatial distribution, Rio de Janeiro.

THE SPATIAL DISTRIBUTION OF PLANTS within a population is first determined by the distribution of seeds during seed dispersal (Clark & Clark 1984). Seed dispersal is the last step in the reproductive cycle of plants, but also the starting point in the process of population renewal and recruitment (Herrera *et al.* 1994). The seed shadow of tree species is spatially unpredictable because it is a function of the efficiency of the dispersal agents, and of the parent's productivity (Janzen 1970), as well as soil condition and micro topography (Loiselle *et al.* 1996). Post dispersal seed distribution is important because the growth and survival of plants depend on the location reached by the seeds (Schupp 1988).

The probability of seeds falling far from the parent plants is dependent on its size or mass. Usually a very large fraction of the total seeds falls close to the parental tree (Howe *et al.* 1985; Forget 1989), and the probability of this happening must be considerably greater for heavy seeds dispersed by gravity (Richard 1996). Seed dispersal by gravity or barochory is often characteristic of huge fruit that do not show any other morphological features enabling them to be primarily dispersed by biotic (bats, birds, monkeys, elephants, rodents) or abiotic (explosion, wind, water) agents (Sabatier 1983 *apud* Forget 1992b). According to Denslow (1980), the seed and perhaps seedlings shadow of species that bear heavy fruit, are expected to be correlated to the area of the parental crown and to topography.

So, the goal of this study was to describe the spatial distribution of *E. glaziovii* fruit and offspring in order to answer the following questions: (1) Does the size of the parental crowns have any influence on the spatial distribution of its fruit and offspring? (2) Does the topography have any influence on the spatial distribution of the *E. glaziovii* fruit and offspring?

MATERIALS AND METHODS

Study area --The study was carried out in four circular plots with 30 m of radius centered on a reproductive tree of *E. glaziovii*. Three of them (B1, B2 and B3) were in the Biological Reserve of Poço das Antas (BIORE) (22°29' - 22°36'S, 42°13' - 42°21'W) and one of them (R1) in the National Park of Tijuca, near the Rio de Janeiro Botanical Garden (RJBG) (22°58'S, 43°13'W) in Rio de Janeiro State, Brazil. Both areas are at evergreen forest, or Ombrophilous Dense Forest (*sensu* Velloso *et al.* 1991). At the BIORE, the mean annual temperature is 27.6°C in summer and 21.3°C in winter, and the mean annual rainfall is 2091.9 mm (IBDF 1981b and data from the Golden Lion Tamarin Association obtained from 1983 to 1998). At the RJBG, the mean annual temperature is 29°C in summer and 22°C in winter, and the mean annual rainfall is 1075 mm (IBDF 1981a; Coelho Neto 1985 *apud* Oliveira & Lacerda 1988).

All the reproductive trees that were found, were sampled and were isolated and very far from one another. The four plots were very distant from each other, from 126 km between the BIORE and the RJBG to 2.5 - 10 km among the BIORE trees. All studied plots were in slope areas (chapter 1). Furthermore, three plots presented values of canopy coverage >80%. However, one of them (B2) presented values of canopy coverage < 80% out of the central reproductive tree crown, with high variation, while under the crown, the canopy coverage values were >80%. None of the plots presented seasonal variations in canopy coverage (chapter 1).

Studied species. -- *Enterolobium* (Mimosaceae) is a neotropical genus distributed from Central America (Mexico) to South America (Argentina) in which the Amazon is it center of diversity (Mesquita 1990). Timber of this genus is used to make boats, packing cases and scantlings. The species are separated mainly by fruit morphology, which are predominantly indehiscent. Among the 10 species of the genus, *E. glaziovii* presents restrict geographic distribution, it has only been sampled in three states of Brazil: Rio de Janeiro, Espirito Santo and Bahia, being endemic of the Brazilian Coastal Atlantic forests (Mesquita 1990). It occurs at a low frequency in forest sites (Lima, H. C. Botanical Garden of Rio de Janeiro, Brazil, pers. comm.). It is a deciduous canopy tree, and its reproductive individuals range from 8 to 30 m tall (Mesquita 1990). Fruit fall yearly around May and June and the tree loses its leaves in May, June and July. Fruit are large and heavy (14.6 g ±6.4), they are contorted black woody, of 8-10 cm x 4-5 cm (Mesquita 1990), containing 1 to 14 seeds, with a mean of 9 seeds per fruit (Ramos & Andrade unpubl. data). No record of predation on *E. glaziovii* seeds inside the fallen fruit was made in the study area (Ramos & Andrade unpubl. data).

Crown size --In order to evaluate the effect of the size and asymmetry of parental crowns on the spatial distribution of the *E. glaziovii* fruit and offspring, each crown was divided into in eight irregular triangles and the area (m^2) of each triangle was calculated by trigonometric relations. The distance from the bole to the crown edges of the central reproductive tree was measured constructing a system of four wedges of 90° at each four compass directions (N, L, S, O). The crown asymmetry was obtained by dividing the crown in two halves, considering the maximum value among the possible pairs. The maximum value was calculated dividing the largest of these two halves by the total area (A_{max} / A_{total}). This value varied between 0.5 (symmetry) and 1.0 ("complete" asymmetry) (Young & Perkocha 1994). The fruit and offspring number of *E. glaziovii* was obtained from under and out of the central reproductive tree and under each of the four crown triangles.

Topography --In order to evaluate the influence of the topography on the spatial distribution of the *E. glaziovii* fruit and offspring, all the plots, which were in slope areas, were separated in two sub-plots, on up-slope direction (areas above the central reproductive tree), and in another two sub-plots on down-slope direction (areas below the central reproductive tree). The fruit and offspring numbers of *E. glaziovii* were obtained inside each sub-plot.

Fruit and offspring distribution –The offspring number of *E. glaziovii* was obtained in circular plots from 1996 to 1999. However, the fruit number was sampled inside each circular plot, by four 30 m long wedges of 5°, in each of the four compass directions away from each central reproductive tree. The fruit number and its distance from the parental tree were just recorded in 1998 and 1999, as soon as their fruit dropped. No seed were observed out of the fruit.

Statistical analysis --The mean numbers of fruit and offspring were calculated among the years. After an arcsine transformation, the data were subjected to *t* tests in order to compare the mean numbers of fruit and offspring between under and out of the parental crown, and between up and down-slope directions (Zar 1996). Pearson correlation coefficient was used in order to test the relationship between the area of each parental crown triangles and the mean number of fruit (among years) and between the area of each parental crown triangles and the mean number of offspring (among years) under it. Pearson correlation coefficient was also used to test the relationship between the median distance of the fruits from the parental tree and the size of the radii of the parental crown. The values of the crown triangle area were subjected to square root transformation and the mean number of fruit and offspring suffer arcsine transformation before the correlation test.

RESULTS

Crown size --The mean crown radii of each central reproductive tree ranged from 5.14 to 12.43 m and the crown area of each one ranged from 163.14 to 541.17 m^2. All central reproductive trees had asymmetric crowns, offset on down-slope directions (table 1). In its turn, there were more fruit ($t = 3.7$; DF = 6; p = 0.05) and more offspring number ($t = 6.3$; DF = 6; p = 0.001) under the parental crown than outside of it (figure 1). The parental crowns that had greater areas also presented greater number of fruit (r = 0.62; DF = 14) and offspring (r = 0.51; DF = 14) under it. All *E. glaziovii* offspring were under canopy coverage above 80%. In B2, although out of the central reproductive tree crown presented canopy coverage values below 80% (*see* study area), all the *E. glaziovii* offspring (100%) was under it.

Topography -- There was significantly greater number of fruit ($t = 89.5$; DF = 6; p = 0.001) and offspring ($t = 20.1$; DF = 6; p = 0.001) on down than up-slope direction (figure 2). However, there was no correlation between the radii of the parental crown and the median of fruit distance from the parental bole (r = 0.40; DF = 6) in the sub-plots of down-slope direction. In other words, greater crown radii did not represent an increase in the median distance of the fruit, from the bole to down-slope directions.

DISCUSSION

Fruit clump under parental plants, such as *E. glaziovii*, has been found in many plant species, specially heavy fruit with no apparent means of dispersal (Forget 1989; Forget 1992b; Herrera *et. al*. 1994, Negi *et al.* 1996). For example, in the French Guiana, *Eperua grandiflora* presented most of its fruit under the parental crown (Forget 1992a). And, Laman (1996) working in a Bornean rain forest, found in two *Ficus* species (which bear small fruit) that more than 50% of its fruit fell under their own crown. Moreover, the shape and size of the adult crown may influence the seed distribution on the soil (Ramirez & Arroyo 1987). These authors showed that *Copaifera publiflora* trees with smaller crown area presented greater seed density at the crown edge, while trees with larger crown area presented greater seed density near the trunk.

Offspring from barochoric species is, in general, well adapted to establish and grow near parental tree, in environment with low light intensity (Forget 1992). Studies following seed rain and seedling survivorship have shown that early seedling recruitment may be spatially correlated with seed rain, although this concordance may vanish as seedling age and establish as sapling (Herrera *et al.* 1994).

On the other hand, slope presents a strong influence on fruit and seed shadow of barochoric species, because when the fruit fall on the ground they can roll down the slope (Forget 1992a). The rain and trampling by animals are other factors that could contribute to the fruit becoming oriented to down-slope directions. Fruit and offspring oriented to down-slope direction, presented by *E. glaziovii* in this study, was also found in two species that bear large fruit, one Bombacaceae in Colombia (Denslow 1980), and *Eperua grandiflora* (Ceasalpinaceae) in the French Guiana (Forget 1992a).

Although there was high variation in the declivity among the studied plots, all of them were at slope areas (*see* study area). Nevertheless, if most of the fruit and offspring are on down-slope direction, what are the factors that maintain this species in a slope area and hinder it from descending until a flat area? According to Forget (1992a), the secondary disperser might compensate this fact by distributing the fruit and seeds more homogeneously between down and up-slope directions. The secondary seed dispersal on the upper side of the slope might promote a slow ridge colonization process, and compensate for the slope effect that drives most of the seeds to land down the slope (Forget 1992b). However, the seed shadow in the study plots probably has been very little influenced by frugivorous animals. In all the plots there was a great concentration of fruit on the ground and they had been untouched through time (more than one year). Other fact that reinforces this supposition is the hunting activity inside the two reserves where the plots were located (IBAMA pers. com.), which can be reducing the populations of *E. glaziovii* fruit consumers. Therefore, these results indicate that both the size of the parental crown and the topography have influence on the spatial distribution of the *E. glaziovii* fruit and offspring.

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Table 1: Characteristics of the central reproductive tree crowns at R1, B1, B2 and B3: their mean (±SD) crown radii, crown asymmetry values, and also the direction (N = North, NE = Northeast, SW = Southwest) of their crowns orientation (d = down-slope direction). R1 was in the National Park of Tijuca, near the Rio de Janeiro Botanical Garden (RJBG), and B1, B2 and B3 were at the Biological Reserve of Poço das Antas (BIORE) in Rio de Janeiro State, Brazil.

	R1	**B1**	**B2**	**B3**
Mean crown radii (m)	7.2 (± 5.4)	9.1 (± 2.4)	12.4 (± 1.8)	5.2 (±2.3)
Crown area (m^2)	235.0	311.9	541.2	163.2
Crown asymmetry	0.94	0.71	0.67	0.77
Asymmetry direction	N (d)	NE (d)	SW (d)	N (d)

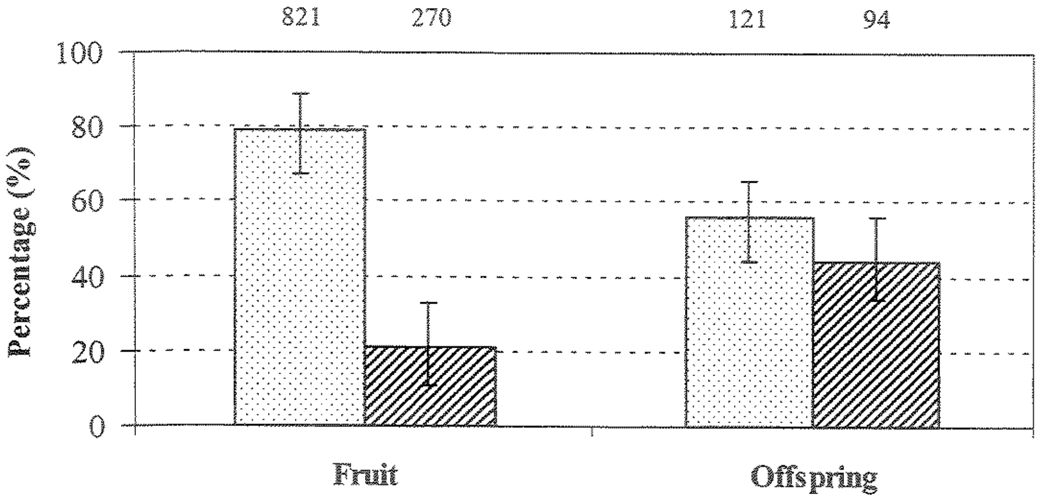

Figure 1: Percentage (mean ± SD) of the *E. glaziovii* fruit and offspring under (doted bars) and out (hatched bars) of the central reproductive tree crown and its sample numbers on each bar. These data were the mean number of fruit from 1998 to 1999, and mean number of offspring between 1996 and 1999. There was difference between the number of fruit (t = 3.7; DF = 6; p = 0.05) and offspring (t = 6.3; DF = 6; p = 0.001) under and out of the parental crown.

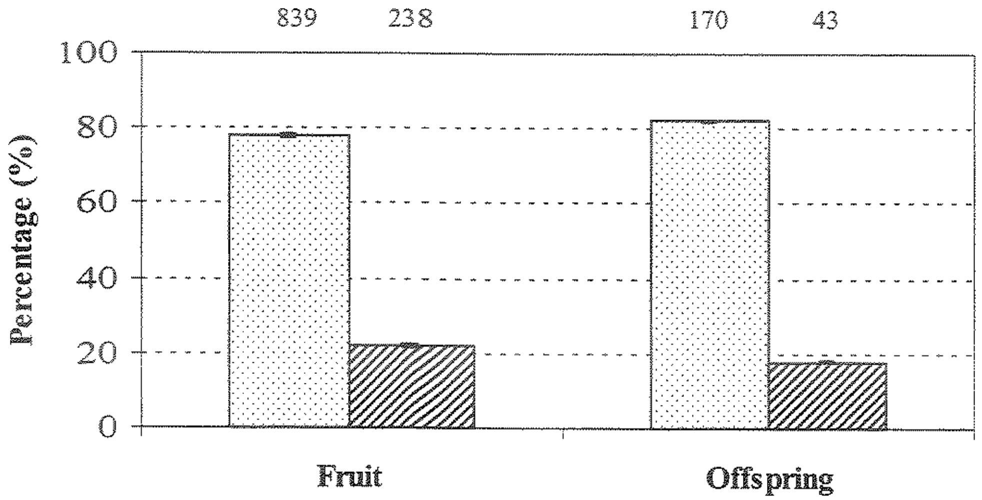

Figure 2: Percentage (mean ± SD) of the *E. glaziovii* fruit and offspring on down (dotted bars) and up-slope (hatched bars) direction and its sample numbers on each bar. These data were the mean number of fruit from 1998 to 1999, and of offspring from 1996 to 1999, after a re-transformation from arcsine. There was difference in fruit (t = 89.5; DF = 6; p = 0.001) and offspring (t = 20.1; DF = 6; p = 0.001) number between on down and up-slope direction.

CAPÍTULO 3

OFFSPRING GROWTH OF *Enterolobium glaziovii* Bentham (MIMOSACEAE)[1]

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[1]- Nos moldes da revista American Journal of Botany.

RESUMO

O objetivo deste estudo foi investigar: (1) se o crescimento de jovens de *Enterolobium glaziovii* difere entre indivíduos localizados embaixo e fora da copa da planta parental; (2) se o crescimento de jovens difere entre parcelas com alta e baixa densidade de coespecíficos e; (3) se o crescimento de plântulas de *E. glaziovii* difere sob diferentes níveis de sombreamento. Para isso, todos os jovens dentro de quatro parcelas circulares de 30 m de raio, centralizadas em um adulto de *E. glaziovii*, foram marcados e tiveram suas alturas medidas anualmente entre 1996 e 1999. As parcelas se localizam no estado do Rio de Janeiro (22°29' - 22°36'S, 42°13' - 42°21'W e 22°58'S, 43°13'W), Brasil. Além disso, o crescimento de plântulas submetidas a cinco tratamentos com diferentes níveis de sombreamento (90%, 80%, 60%, 40% e 0%) foi acompanhado na casa de vegetação. A altura e o diâmetro do colo de cada plântula foram medidos mensalmente durante seis meses. O peso seco das folhas, caule e raízes das plântulas foram obtidos no começo, com plântulas separadas das usadas nos tratamentos, e após o término do experimento. Embaixo da copa da planta parental, em parcelas com alta densidade, a maioria dos jovens apresentou pequenos incrementos de altura, enquanto que nas parcelas com baixa densidade, o crescimento foi mais variável entre os jovens. As plântulas de *E. glaziovii* sobreviveram e cresceram em todos os tratamentos de sombreamento. Porém as que cresceram a 90% e 80% de sombreamento apresentaram um incremento em altura maior do que nos outros tratamentos, sem sofrerem estiolamento. Os dados parecem indicar que o crescimento dos jovens de *E. glaziovii* é afetado negativamente pela densidade de coespecíficos, enquanto que o efeito da cobertura da copa da planta parental parece não ser importante. As plântulas desta espécie são capazes de sobreviver e crescer em uma grande amplitude de sombreamento por pelo menos 6 meses, mas apresentam maior incremento de altura em ambientes com mais de 80% de cobertura.

ABSTRACT

The aims of the present study were answer the following questions: (1) was there difference in the growth of *Enterolobium glaziovii* offspring under and out of the parental crown? (2) Was there difference in the growth of *E. glaziovii* offspring between forest sites with high and low conspecific offspring density? (3) Was there any difference in growth of its seedling under different shade levels? All *E. glaziovii* offspring in four circular plots, which were centered in a reproductive tree of the same species, were tagged and their height were measured yearly, from 1996 to 1999. The study was carried out in Rio de Janeiro State (22°29' - 22°58'S and 42°13' - 43°13'W), SE, Brazil. Furthermore, *E. glaziovii* seedling growth was evaluated in five treatments, each one with different shade levels (90%, 80%, 60%, 40% and 0%) in a greenhouse. Although, in plots with high conspecific density the offspring growth was greater under than out of the parental crown, there was no such difference in low density plots. The seedlings survived and grew in all shade treatments. However, the ones that grew at 90% and 80% of shade presented greater height increment than the other treatments, without been etiolated. It seems that *E. glaziovii*'s offspring growth is negatively affected by conspecific density, while the parental effect is not important. Seedlings of this species are capable of survive and grow in a broad range of shade levels, at least for 6 months.

Keywords: conspecific influence, *Enterolobium*, growth, low light environment, Mimosaceae, seedling, shade tolerance.

All living organisms are, at various stages in their life, capable of "growth" in the sense of change in size and in form given suitable conditions (Hunt, 1982). In tropical rain forest, light is one of the most limiting factors affecting plant growth and survival (Poorter, 1999) because it is the major determinant of seedling photosynthesis and growth, and affects the allocation of biomass to different plant parts (Roos and Quinn, 1977, Swaine *et al.*, 1997). Veneklaas and Poorter, (1998 *apud* Poorter, 1999) in a literature compilation on growth of tropical tree seedlings, found that all growth related plant traits were influenced by light.

Although the seeds of many rain forest canopy trees are able to germinate in the forest understory (Garwood, 1983), growth and survival rates of seedlings are often low, unless they occur in or near treefall gaps (Augspurger, 1984). The few seedlings that do survive in the understory are very important in forest dynamics, because suppressed seedlings and saplings are a major component of the regrowth that occurs in new treefall gaps (Brokaw, 1985). It is crucial to know the growth differences among species, as well as, the factors that could influence it (Hubbell and Foster 1990) in order to give a better understanding of the ecology of these species, in deep forest shade, because the majority of tree seedlings begin life in this environment, where light is the limiting factor and may influence the evolution of the species (Agyeman, Swaine and Thompson, 1999).

The ability of seedlings to grow and survive in the understory environments where light may often be limiting, is one of the conditions for a successful tree regeneration in this environment (Kozlowski, 1971 *apud* Negi, Negi and Singh, 1996; Poorter 1999). Differences in species responses to irradiance are important since the forest light environment is continually changing due to natural tree fall, logging and other disturbances (Swaine *et al.* 1997; Agyeman, Swaine and Thompson, 1999). The relationship between light conditions and tree growth can be used to predict future timber yields in managed forests using an individual-based growth model (Webb, 1999).

The aims of the present study was to answer the following questions: Considering that the *E. glaziovii* offspring were in environments that presented canopy coverage values >80% in the study area (*see* study species) (1) was there difference in the growth of its offspring under and out of the parental crown? (2) Was there difference in the growth of its offspring between forest sites with high and low conspecific offspring density? And (3) was there difference in seedling growth under different shade levels?

MATERIALS AND METHODS

Study species

Enterolobium (Mimosaceae) is a neotropical genus distributed from Central America (Mexico) to South America (Argentina) in which the Amazon is its center of diversity (Mesquita 1990). Timber of this genus is used to make boats, packing cases and scantlings. The species are separated mainly by fruit morphology, which are predominantly indehiscent (*E. glaziovii* is not an exception). Among the 10 species of the genus, *E. glaziovii* presents restrict geographic distribution, it has only been sampled in three states of Brazil: Rio de Janeiro, Espirito Santo and Bahia, being endemic of the Brazilian Coastal

Atlantic forests (Mesquita 1990). It occurs at a low frequency in forest sites (Lima, H. C. Botanical Garden of Rio de Janeiro, Brazil, pers. comm.). It is a deciduous canopy tree, and its reproductive individuals range from 8 to 30 m tall (Mesquita 1990). Fruit are large and heavy (14.6 g ±6.4), they are contorted black woody pods, of 8-10 cm x 4-5 cm (Mesquita 1990), containing 1 to 14 seeds, with a mean of 9 seeds per fruit (Ramos & Andrade unpubl. data). Moreover, all the *E. glaziovii* offspring were in environments with canopy coverage >80% (chapter 2). In addition, there are differences in mortality rates among offspring size. Small *E. glaziovii* (individuals < 15 cm tall) presented significantly greater mortality rate than medium (individuals between 15 and 50 cm tall) and large (individuals >50 cm tall) ones (chapter 4).

Study area

The study was carried out in four circular plots with 30 m of radius centered on a reproductive tree of *E. glaziovii*. Three of them (B1, B2 and B3) were in the Biological Reserve of Poço das Antas (BIORE) (22°29' - 22° 36'S, 42°13' - 42°21'W) and one of them (R1) at National Park of Tijuca, near the Rio de Janeiro Botanical Garden (RJBG) (22°58'S; 43°13'W) in Rio de Janeiro State, SE, Brazil. Both areas are at evergreen forest, or Ombrophilous Dense Forest (*sensu* Velloso *et al.* 1991). At the BIORE, the mean annual temperature is 27.6°C in summer and 21.3°C in winter, and the mean annual rainfall is 2091,9 mm (IBDF 1981b and data from Golden Lion Tamarin Association obtained from 1983 to 1998). At the RJBG, the mean annual temperature is 29°C in summer and 22°C in winter, and the mean annual rainfall is 1075 mm (IBDF 1981a; and Coelho Neto 1985 *apud* Oliveira & Lacerda 1988).

All the reproductive trees that were found, were sampled and were isolated and very far from one another. The four plots were very distant from each other, from 126 km between the BIORE and the RJBG to 2.5 - 10 km among the BIORE trees. All studied plots were in slope areas (chapter 1). Furthermore, three plots presented values of canopy coverage >80%. However, one of them (B2) presented values of canopy coverage < 80% out of the central reproductive tree crown, with high variation, while under the crown, the canopy coverage values were >80%. None of the plots presented seasonal variations in canopy coverage (chapter 1).

Parental effect and offspring density effect

All *E. glaziovii* offspring (non-reproductive individual) in the circular plots were tagged and recorded according it location under and out of the central reproductive tree crown. Their height (from the ground until the apical bud) was measured yearly, from 1996 to 1999. Offspring growth under and out of the central reproductive tree crown was compared between plots with high and low density of conspecific offspring, to distinguish the density and parental effects on offspring growth. The offspring densities in a high density plot (B1) was 0.033 offspring/m^2 under the parental crown, and 0.025 offspring/m^2 out of it. In its turn, the offspring density in low density plot (R1, B2 and B3 together) was 0.008 offspring/m^2 both under and outside of the parental crown. The offspring density was calculated dividing the mean offspring number among the years by the area of the plot (2827.4 m^2).

Shade levels

Considering that canopy coverage could change due to fall of trees and shoots affecting the chances of establishment of individuals, an experiment was carried out in a greenhouse at Universidade Estadual de Campinas, São Paulo State, Brazil, in order to know if the *E. glaziovii* seedlings can grow under different shade levels.

E. glaziovii seeds were collected in the same study area where the field measurements were taken (see below). They were scarified and germinated on vermiculite, in plastic pots in the greenhouse, without both light and temperature control. When they presented a 3 mm radicle, they were planted individually in 500 ml plastic cups filled with 2:1 soil:sand mixture. The soil was collected at the Santa Genebra Reserve (22°44'45"S; 47°06'33" W), in São Paulo State.

The faneroepigeal seedlings (sensu Garwood, 1996) were initially grown in the greenhouse, and when seedlings presented their cotyledons completely expanded they were transferred to boxes covered thin plastic shade cloths. These treatments provided 90%, 80%, 60%, 40% and 0% (full sun) of shade. The irradiance in each box was measured with LI-COR line quantum sensor coupled with LI 1000 data logger. Concurrent measurements were made inside each box and in the open at 12:00 hs on 4 cloudless days. So, the treatments could be expressed as a percentage of shade.

Twenty seedlings per treatment were allocated randomly in five rows of four plastic cups inside each box and were re-randomized every month through the experiment, over six months. The seedling height (until the apical meristem) and the root collar diameter were recorded monthly. Seedlings were watered daily.

Twenty seedlings were harvested on the day that the experiment began and all seedlings of each treatment were harvested at the end of the experiment, after six month. Leaves, stems and roots were dried at 80 °C for 48 h and their dry biomass was obtained. Relative growth rate (RGR) [(ln final dry mass - ln initial dry mass) / period of time], relative leaves mass (RLM) and relative root mass (RRM) (dry mass of leaves or roots / total seedling dry mass), were calculated for each seedling according to Hunt (1982). Stem robustness (SR) (total dry mass / stem length) was calculated according to Lee *et al* (1996).

Statistical analysis

Height increment data did not show a normal distribution. Mann-Whitney test was used to compare the difference in cumulative height increment between offspring under and out of the central reproductive tree crowns, in plots with both high and low offspring density, after a three year interval (Zar 1996). Individuals with null and negative height growth were not considered in the analysis. Furthermore, the Kruskal-Wallis test followed by the Dunn multiple comparison test (Zar 1996) was used in order to compare all the growth parameters obtained from the shade treatments in the greenhouse experiments.

RESULTS

Parental effects and offspring density effect

Although plots with low conspecific offspring density did not presented any difference between offspring growth under and out of the parental crown (U = 1.4; DF = 1; p = 0.16), plots with high conspecific offspring density had the opposite result (U = 4.9; DF = 1; p = 0.0001). Under the parental crown, in the plot with high conspecific offspring density most of the offspring presented smaller height increment than in plots with low offspring density (U = 22.3; DF = 1; p = 0.026) (fig. 1). On the other hand, out of the parental crown, there was no difference in the offspring growth between the plots with high and low offspring density (U = 1.52; DF = 1; p = 0.13).

Shade levels

After 65 days no *E. glaziovii* seedlings presented cotyledons. On the other hand, *E. glaziovii* survived and grew under all shade treatments, but there were differences on growth among them. The seedlings at 90% e 80% of shade presented significantly higher height growth than the other treatments (H= 31.8; df= 4; P= 0.001), although there was no significant difference in stem diameter growth among them (H = 3.37; DF= 4; P= 0.50). There were differences in stem robustness (H = 10.0; DF= 4; P= 0.004) among the treatments, except for seedlings at 90% and 0% treatments. Thus, seedlings at 90% of shade were not etiolated, although they presented the greatest height growth, and they did not have any difference on the total dry mass among the other shade treatments. Under all treatments the seedlings produced similar total biomass (H = 6.0; DF= 4; P= 0.20), and presented similar RGR (H = 4.6; DF= 4; P= 0.33) among them. The allocation of the biomass for roots (RRM) (H = 25.9; DF= 4; P= 0.001) and for leaves (RLM) (H = 18.8; DF= 4; P= 0.001) in seedlings differed among the treatments (table 1). The seedlings under 0% of shade had greater relative root mass (RRM), while seedlings under 90% of shade had greater relative leave mass (RLM) than the seedlings in the other treatments (table 1).

DISCUSSION

Rain forest tree species are often classified into two functional groups based on their germination and establishment requirements (Swaine and Whitmore 1988; Whitmore, 1996). Shade-tolerant species can germinate, grow and survive in environments of low light intensity, whereas light demanding species need environment of high light intensity for establishment (Poorter, 1999). The shade-tolerant species constitute the vast majority of the tropical-forest tree species (Welden *et al.*, 1991; Clark and Clark, 1992). In a rain forest in Panama, for example, saplings of 79% of the species were shade-tolerant (Welden *et al.*, 1991). In its turn, *E. glaziovii* presents characteristics of a shade-tolerant, "non-gap" species. It is capable of germinate (Ramos and Andrade unplubl. data) and growth in environments of low light intensities.

On the other hand, the growth of *E. glaziovii* offspring was negatively affected by conspecific density, but not by parental tree. The *E. glaziovii* offspring growth under the parental crown was just affected in plots with high density, but out of the parental crown, there was no difference between offspring growth in plots with high and low offspring density. Because, out of the parental crown, there was no difference in the offspring growth between plots with high and low offspring density. According to Condit *et al.* (1994) density dependent factors could regulate population sizes, due to both intraspecific competition caused by direct interference among near neighbors, as well as to the attraction of density-responsive natural enemies (Howe *et al.* 1985). The density effect could increase the mortality probabilities of *E. glaziovii* offspring under high conspecific density. The *E. glaziovii* offspring at high conspecific density grow slowly and consequently stay longer in a small size class, which has greater mortality rate.

In the greenhouse, the *E. glaziovii* seedlings grew under a broad range of shade levels. However, they presented traits of shade-tolerant species, such as higher growth under 90% and 80% of shade, without presenting etiolation. Seedlings of *E. glaziovii* had no statistical difference on RGR among the shade treatments (90% - 0%). According to

Crawford (1989) the shade plants are able to maintain a constant relative growth rate (RGR) under light intensities that ranges from full sun to moderate shade. Shade tolerance in species is not related to growth but to persistence (Paccala *et al.*, 1996). It is suggested that these species do not maximize their potential growth rate, but rather their realized biomass growth under field conditions (Kitajima, 1996 *apud* Poorter, 1999).

The differential biomass allocation between shaded seedlings of *E. glaziovii* (90%) and the lighted ones (0%) is normally found in plants growing in different irradiance environment (Agyeman, Swaine and Thompson, 1999). Plants under shaded treatments tend to enhance their light interception steering a higher biomass allocation to leaves (Popma and Bongers, 1988; Crawford, 1989), while plants at lighted ones, on the other hand, are faced with high radiation loads. Thus, they tend to invest more in root mass, in a way that compensates for higher transpiration losses by water uptake (Veenendaal *et al.*, 1996).

Despite the fact of the *E. glaziovii* seedlings survived under 0% of shade (full sun), in the greenhouse experiment, no individual of the studied species was found in this environment in forest sites. Probably other environmental variables are also important factors influencing the offspring growth. According to Swaine *et al.* (1997), the response to irradiance of offspring, in a greenhouse, may be modified by mycorrhizal infection and by the success with which plant roots explore the soil resources and harvest nutrients in the presence of competing species, in forest sites. The root competition might also influence the growth and survival of tree seedlings (Denslow, Newell and Ellison, 1991).

Therefore, it seems that the *E. glaziovii* offspring growth is negatively affected by conspecific density, while the parental effect is not important to it. In its turn, seedlings of this species are capable of survive and grow under a broad range of shade levels, for at least 6 months, but they present greater height increments in environments of >80% of shade.

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Table 1: Medians, minimal (Min) and maximum (Max) values of height (cm), collar diameter (cm), total dry mass (g) (TDM), root mass ratio (g) (RMR), leaf mass ratio (g) (LMR), relative growth ratio (g g^{-1} month^{-1}) (RGR) and stem robustness (g g^{-1}) (SR) of each shade treatment. In each row, different letters regard statistical difference of 5% of significance on the Kruskal-Wallis test.

	90%			80%			60%			40%			0%		
	Min	**Median**	**Max**	**Min**	**Median**	**Max**	**Min**	**Median**	**Max**	**Min**	**Median**	**Max**	**Min**	**Median**	**Max**
Height	1.4	4.1 ^{b}	5.6	1.4	3.9 ^{b}	5.6	1.2	2.6 ^{a}	5.6	1.9	2.6 ^{a}	4.2	0.8	2.5 ^{a}	3.7
Diameter	0.04	0.10 ^{a}	0.19	0.0	0.12 ^{a}	0.19	0.05	0.10 ^{a}	0.20	0.08	0.11 ^{a}	0.19	0.07	0.09 ^{a}	0.15
TDM	0.34	0.53 ^{a}	1.72	0.12	0.61 ^{a}	1.32	0.21	0.58 ^{a}	1.52	0.25	0.54 ^{a}	1.19	0.10	0.44 ^{a}	0.72
RRM	0.27	0.40 ^{a}	0.52	0.29	0.38 ^{a}	0.52	0.33	0.42 ^{a}	0.59	0.36	0.47 ^{ab}	0.51	0.33	0.51 ^{b}	0.61
RLM	0.34	0.46 ^{b}	0.6	0.26	0.49 ^{b}	0.60	0.30	0.46 ^{ab}	0.54	0.24	0.42 ^{ab}	0.54	0.23	0.38 ^{a}	0.52
RGR	0.32	0.42 ^{a}	0.60	0.18	0.45 ^{a}	0.61	0.17	0.44 ^{a}	0.60	0.26	0.46 ^{a}	0.60	0.14	0.41 ^{a}	0.55
SR	0.006	0.009 ^{a}	0.021	0.005	0.009 ^{ab}	0.026	0.05	0.010 ^{b}	0.018	0.08	0.011 ^{b}	0.016	0.005	0.008 ^{a}	0.016

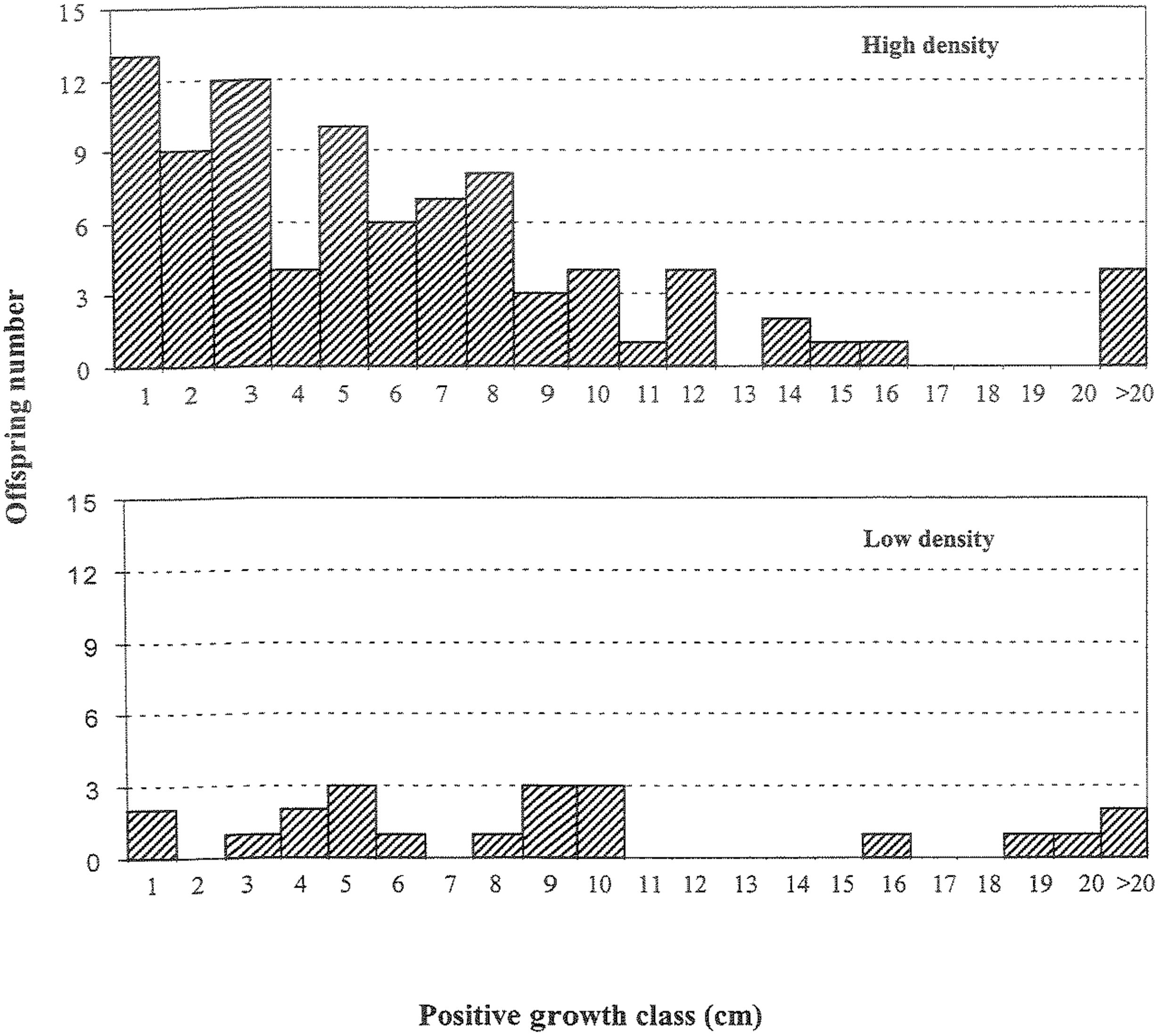

Figure 1: Offspring number in each cumulative (from 1996 to 1999) positive growth class (cm) under the parental crown, in plots with high (B1) and low offspring density (R1, B2 and B3 together). There was difference by Mann-Whitney test.

CAPÍTULO 4

RECRUITMENT AND MORTALITY OF OFFSPRING OF *Enterolobium glaziovii* (MIMOSACEAE) AROUND REPRODUCTIVE TREES[1]

1- Nos moldes da revista Journal of Ecology.

Resumo

Segundo a hipótese de Janzen-Connell a distribuição espacial das populações de plantas é dependente da densidade de sementes e plântulas e das distância da planta mãe. E, em geral, há uma mortalidade diferencial entre plantas de tamanhos diferentes. Portanto, o objetivo deste trabalho foi responder às seguintes questões: (1) a taxa de mortalidade difere entre jovens de *Enterolobium glaziovii* de tamanhos diferentes? (2) O recrutamento de novos indivíduos é diferente embaixo e fora da copa da planta parental? (3) O recrutamento de novos indivíduos difere entre parcelas com alta e baixa densidade de frutos coespecíficos? (4) As taxas de mortalidade dos jovens de *E. glaziovii* diferem embaixo e fora da copa da planta parental? (5) As taxas de mortalidade dos jovens de *E. glaziovii* diferem entre parcelas com alta e baixa densidade de jovens coespecíficos? O trabalho foi realizado no estado do Rio de Janeiro (22°29' - 22°58'S and 42°13' - 43°13'W), Brasil. Todos os jovens de *E. glaziovii* foram amostrados e marcados dentro de quatro parcelas circulares de 30 m de raio, cada uma delas centralizada em um adulto de *E. glaziovii*, de 1996 a 1999. O número de frutos foi amostrado através de 4 setores em cada parcela (155.5 m^2). O recrutamento (indivíduos pequenos ausentes no censo anterior) e a mortalidade dos jovens marcados foram acompanhados durante todo o período de estudo. Considerando três classes de tamanho de jovens (pequeno = < 15 cm de altura, médio = entre 15 e 50 cm de altura e, grande = > que 50 cm de altura), a taxa anual de mortalidade de indivíduos pequenos foi significativamente maior do que as taxas dos indivíduos médios e grandes. Os primeiros três meses foram críticos para os novos indivíduos, pois cerca de 55% deles morreram neste período. Não houve diferença entre o recrutamento observado e esperado (estimado pelo número de frutos amostrado) tanto embaixo e fora da copa da planta parental, como em parcelas com alta e baixa densidade de frutos. Danos físicos pela queda de galhos foi um fator importante de mortalidade, responsável por cerca de 10 a 23% da mortalidade anual de jovens. Não houve diferença entre a taxa de mortalidade dos jovens embaixo e fora da copa da planta parental e entre a taxa em parcelas com parcelas com alta e baixa densidade de coespecíficos. Portanto há mortaliade diferencial entre os tamanhos de jovens de *E. glaziovii.* E nem o recrutamento, nem a taxa de mortalidade de jovens desta espécie são negativamente afetados embaixo da copa da planta parental, ou em parcelas com alta densidade de jovens.

Summary

1. According to Janzen-Connell hypothesis, the plants spatial distribution is dependent on the density of dispersed seeds and seedlings and its distance from the parent tree. And, in general, there is differential mortality among offspring sizes. Hence, we document the recruitment of new individuals and the mortality rates of *E. glaziovii* offspring and evaluate their relationship on the natural regeneration of this species.

2. All *E. glaziovii* offspring were tagged, and evaluated in four circular plots, with 30 m of radius centred in a reproductive tree of *E. glaziovii,* from 1996 to 1999. In each plot, the number of *E. glaziovii* fruit was sampled under and out of the parental tree crown with the aid of four wedges ($155.5m^2$). New recruitment and offspring mortality were recorded uring the study, which was carried out in Rio de Janeiro State (22°29' - 22°58'S and 42°13' - 43°13'W), SE, Brazil. The *E. glaziovii* offspring were divided in three size classes: small (individuals < 15 cm tall), medium (individuals from 15 to 50 cm tall) and large (individuals >50 cm tall) and their mortality rates were compared. Small individuals presented higher annual mortality rate than medium and large ones.

3. There was no significant difference between the recruitment both under and out of the parental crown and in plots with high and low density of conspecific fruit. There were no differences between annual mortality rate of offspring under and out of the central reproductive tree crown and between plots with high and low density of conspecific offspring

4. Therefore there is differential mortality among offspring sizes of *E. glaziovii.* And the recruitment and the offspring mortality rate, of this species, are not negatively affected either by offspring density or under parental crown.

Keyword: Density-dependence mortality, distance-dependence mortality, litterfall damage, recruitment, size-dependent mortality, seedling.

Introduction

Spatial distribution of plant populations is dependent on two interacting functions, the density of dispersed seeds and seedlings and their distance from the parent tree (Janzen 1970). Janzen (1970) and Connell (1971) suggested that due to the high seed rain beneath fruiting trees, density or distance responsive predators and pathogens tend to concentrate near the parent trees where seed and seedling mortality is virtually complete. Propagules dispersed far from the parent plant, on the other hand, are much more likely to escape predation and thus have a higher survivorship. High seedling recruitment may therefore occur at some distance away from, rather than beneath or adjacent to the parental plant. Hubbell (1979, 1980) reviewed the qualitative model of Janzen (1970) and suggested that unless mortality is 100% near the parent tree, most of the recruited offspring will be near the parent. He reasoned that seed density is very high near the parent relative and even if high mortality occurs near the parent tree, a very small percentage of survivorship, will generate greater numbers of seedlings than a larger percentage of survivorship at a farther distance (Augspurger 1983, Cintra 1997). This altered model may then explain the finding that the majority of tree species in tropical forests have clumped distribution (Hubbell 1979, Armesto *et al.* 1986).

In its turn, there are few studies on critical demographic stages for tropical tree species on literature, such as seedling recruitment (Schupp 1990). The amount and the spatial pattern of seedling recruitment are influenced heavily by seed distribution at the time of its dispersal (Augspurger 1983, 1984). Knowledge of the factors influencing seedling mortality, which is very high (Clark & Clark 1985), will lead to better understanding of the process of natural regeneration of trees, and has practical applications in the management of forests to favour the regeneration of desired timber species (Still 1996).

Thus, here we document the recruitment of new individuals and the mortality rates of *E. glaziovii* offspring and evaluate the relationship of these processes to the natural regeneration of this species. This species occurs at low density with its adults are very far from another one. The goal of this study was to answer the following questions: (1) are there differential mortality rates among *E. glaziovii* offspring of different sizes? (2) Is the recruitment of new individuals different under and out of the parental crown? (3) Is the recruitment of new individuals different in plots with high and low density of conspecific fruit? (4) Are the mortality rates of *E. glaziovii* offspring different under and out of the parental crown? (5) Are the mortality rates of *E. glaziovii* offspring different between plots with high and low conspecific offspring density?

Materials and methods

STUDY AREA

The study was carried out in four circular plots with 30 m of radius centered on a reproductive tree of *E. glaziovii*. Three of them (B1, B2 and B3) were in the Biological Reserve of Poço das Antas (BIORE) (22°29' - 22° 36'S, 42°13' - 42°21'W) and one of them (R1) at National Park of Tijuca, near the Rio de Janeiro Botanical Garden (RJBG) (22°58'S; 43°13'W) in Rio de Janeiro State, SE, Brazil. Both areas are at evergreen forest, or Ombrophilous Dense Forest (*sensu* Velloso *et al.* 1991). At the BIORE, the mean annual temperature is 27.6°C in summer and 21.3°C in winter, and the mean annual rainfall is 2091,9 mm (IBDF 1981b and data from Golden Lion Tamarin Association obtained from 1983 to 1998). At the RJBG, the mean annual temperature is 29°C in summer and 22°C in winter, and the mean annual rainfall is 1075 mm (IBDF 1981a; and Coelho Neto 1985 *apud* Oliveira & Lacerda 1988). All the reproductive trees that were found, were sampled and were isolated and very far from one another. The four plots were very distant from each other, from 126 km between the BIORE and the RJBG to 2.5 - 10 km among the BIORE trees.

STUDY SPECIES

Enterolobium (Mimosaceae) is a neotropical genus distributed from Central America (Mexico) to South America (Argentina) in which the Amazon is its center of diversity (Mesquita 1990). Timber of this genus is used to make boats, packing cases and scantlings. The species are separated mainly by fruit morphology, which are predominantly indehiscent (*E. glaziovii* is not an exception). Among the 10 species of the genus, *E. glaziovii* presents restrict geographic distribution, it has only been sampled in three states of

Brazil: Rio de Janeiro, Espirito Santo and Bahia, being endemic of the Brazilian Coastal Atlantic forests (Mesquita 1990). It occurs at a low frequency in forest sites (Lima, H. C. Botanical Garden of Rio de Janeiro, Brazil, pers. comm.). It is a deciduous canopy tree, and its reproductive individuals range from 8 to 30 m tall (Mesquita 1990). Fruit are large and heavy (14.6 g ±6.4), they are contorted black woody pods, of 8-10 cm x 4-5 cm (Mesquita 1990), containing 1 to 14 seeds, with a mean of 9 seeds per fruit (Ramos & Andrade unpubl. data).

OFFSPRING SIZE CLASSES

All *E. glaziovii* offspring in the circular plots were tagged, and evaluated under and out of the parental tree crown. Their height (until the apical bud) was measured yearly, from 1996 to 1999. In order to investiate if there was differential mortality rate among different sizes of *E. glaziovii* offspring, individuals were divided in three size classes: small (individuals < 15 cm tall), medium (individuals from 15 to 50 cm tall) and large (individuals >50 cm tall). Annual mortality rate (*see* below) and survivorship curves for offspring of the first census (1996) were drawn for each offspring size class.

RECRUITMENT

In each season (every 3 months), offspring survival and new recruitments (small individuals that were absent in preceding census) were recorded during the period of study. The expected recruitment was estimated by the mean number of fruit sampled, considering constant the number of seeds per fruit and germination rates and compared with the observed, in order to test differences between under and out of the parental crown and between plots with high and low density of conspecific fruit. The observed recruitments was a mean of new small individuals sampled from 1996 to 1999, the mean number of fruit was calculated from samples in 1998 and 1999.

The number of *E. glaziovii* fruit was sampled with the aid of four 30 m long wedges of 5°, in each of the four compass directions away from each parental tree. The number of fruit in each wedge, under and out of the parental tree was recorded in 1998 and 1999, as soon as their seeds fell.

MORTALITY

Mortality was defined as death or disappearance. The agents of death were recorded as litterfall or unknown. We considered that *E. glaziovii* offspring died due to litterfall when there were fallen trunks or branches near or over snapped individuals, and when some of them died some time later after a palm leave had fallen over it. Stems that snapped but resprouted were considered alive.

Annual mortality rate was calculated in the entire period of the study (from 1996 to 1999), among the three different classes, under and out of the parental crown and plots with high and low density of conspecific offspring. Mortality rate m was calculated as:

$$m = (\ln(N_o) - \ln(N_t)) / t \qquad \text{(Eq 1)},$$

where N_o is the number of initial *E. glaziovii* individuals, N_t the number that remained alive at year t, and $\ln(N)$ is the natural logarithm of N according to Swaine & Lieberman (1987).

DENSITY

Two groups of plots were separated by fruit and offspring densities. Plots with high density of *E. glaziovii* fruit (B1 and B2) had 6.66 fruit/m^2, while plots with low density of fruit (R1 and B3) had 0.35 fruit/m^2. The fruit density was obtained dividing the mean fruit number from 1998 to 1999 by the area of the four wedges (155.5 m^2), in which the fruit were sampled, in each plot.

The plot with higher density of conspecific offspring (B1) had 0.060 offspring/m^2, while the plots with lower density of conspecific offspring (R1, B2 and B3 together) had 0.016 offspring/m^2. The offspring density was obtained dividing the mean offspring number among the years by the area of the plot (2827.4 m^2).

STATISTICAL ANALYSIS

Chi-square test was used to test differences between the numbers of new small individuals recruitment under and out of the parental crown, and in plots with high and low density of conspecific fruit. The Yates correction for continuity was used when the degree of freedom was 1 (Zar 1996). To assess statistical significance of differences in mortality rates, confidence limits (95%) for the mortality rate (according to Condit *et al.* 1995) were calculated using the normal approximation to the binomial variance (Zar 1996). Confidence limits were converted into annual mortality rates using Eq 1. The mean mortality rate under and out of the parental crown, and for plots with high and low conspecific offspring density among years, were compared by the overlaying of their confidence limits. Means, from 1996 to 1999, were compared after arcsine transformation. In its turn, the survivorship curves were statistically compared by log rank test (Hutchings *et al.* 1991).

Results

OFFSPRING SIZE CLASSES

Small individuals presented higher annual mortality rate than medium and large ones (table 1). There was no overlaying confident limit (95%) between the small individuals with the confident limits of medium and large individuals. Nevertheless, there were overlaying confident limits (95%) between the medium and large individuals. On the other hand, although survivorship dropped with time in all classes (Fig. 1), there was significant difference between the small individuals survivorship curve of first census (1996) and the medium and large ones ($LR = 36.2$; $DF = 1$; $p < 0,001$), which, in its turn, did not presented significant difference ($LR = 0.71$; $DF = 1$; $p > 0,75$).

RECRUITMENT

The first three months of life was the most dangerous period to the new small individuals, since about 55% of them died in this period (Fig. 2). There was no significant difference between the expected and observed recruitment number both under and out of the parental crown ($\chi^2 = 1.70$; $DF = 1$; $p= 0.20$), and in plots with high and low density of conspecific fruit ($\chi^2 = 3.3$; $DF = 1$; $p= 0.07$) (table 2). Consequently, there was more recruitment where there was more fruit.

MORTALITY

In most cases, the causes of annual offspring mortality were unknown (about 77 to 90%), but the physical damage by fallen debris, such as branches, palm leaves and other plant parts, was an important annual mortality factor, because it was responsible for about 10 to 23% of the offspring mortality. On the other hand, some medium and large individuals of *E. glaziovii* (about 1 to 9%) were capable of surviving for about 3 to 9 months without any leaves, with the appearance of a dead individual. They seemed to be latent and then, some months later, sprouted new leaves and grew normally.

The annual mortality rate of offspring was not affected neither by offspring density nor under parental crown. There were no differences between the annual mortality rate of offspring under and out of the central reproductive tree crown and between plots with high and low density of conspecific offspring, since there were overlaying confident limits (95%) (table 3).

Discussion

In this study, *Enterolobium glaziovii* followed a well-documented general pattern of size-dependent survivorship in tree populations (Piñero *et al.* 1984, Clark & Clark 1987b, De Steven 1989, Clark & Clark 1992), with small individuals experiencing the greatest mortality. In addition, most of the new small individuals died in the first three months of life. It seems that this is a critical period for *E. glaziovii* and if its small individuals are able to surpass this threshold, their survival chances will increase. In Costa Rica, the mean half-life of the seedlings of 194 species was about 2.5 months (Li *et al.* 1996). According to Clark & Clark (1985) one possible mechanism which increase seedling mortality is the damage to the seedling leaves, due to herbivory or pathogens, which are organs difficult to replace in the highly limited understory. A second potential factor is apical meristem damage.

There are few data both on forest-level rates of physical damage to trees and on the effect of this damage to regeneration (Clark 1990). The mortality rate by this kind of damage found in the present study (10 to 23%) was consistent with other studies. Uhl (1982 apud Clark 1990) found that 38% of the mortality of tree saplings with 1-10 cm of diameter was due to the falling of trees or branches. In Costa Rica, 23% of the stems of six tree species were damaged (Clark & Clark 1987a), while a minimum of 16% of mortality of established seedlings was due to litterfall (Clark & Clark 1987b). This kind of damage was responsible for 9% of *Peltogyne* saplings (0.5 m tall and ≤ 0.64 DBH) mortality in the Maracá Island, N Brazil (Nascimento & Proctor 1997).

In its turn, the recruitment of new small individuals was higher where there were more fruit. In other words, around reproductive individuals of *E. glaziovii* the emergency of new individuals is not affected by the proximity to parental trees, however it is dependent on fruit density. Therefore, the *E. glaziovii* recruitment does not fit the Janzen-Connell hypothesis, which predicts reduction in recruitment probability near adults. According to Condit *et al.* (1992), who investigated the spatial patterns of sapling recruitment in 80 species of trees and shrubs, the majority of the tree species present no clear pattern of recruitment probability (reduction or increment) in the vicinity of large conspecifics.

On the other hand, it seems that neither the offspring density nor the proximity to the parental tree affect the mortality rate of the *E. glaziovii* offspring. Thus, as in the recruitment, the processes predicted by the Janzen-Connell model, with higher seedling mortality beneath the adult trees and under high offspring density, were not operating for *E. glaziovii*. There is evidence that the Janzen-Connell model is not taking place in a number of tropical tree populations (Clark & Clark 1994), such as *Dipterix panamensis* in Peru, that also presented no significant difference in the proportion of seedlings surviving near and far from adult tree (Cintra 1997). Such negative cases may in fact be underrepresented in the literature because they were thought to be less interesting (Clark & Clark 1984).

The *Enterolobium glaziovii* adults were very sparsely distributed in the forest. Nevertheless, neither recruitment nor offspring mortality suffer reduction under the parental tree or related to offspring density. Therefore, it seems that the processes, which occurred at a spatial and temporal scale in this study, did not explain the low density of the *E. glaziovii* adults. Probably, the processes that explain the sparse spatial distribution of the adults may be occurring in a larger spatial and / or temporal scale.

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Table 1: Annual mortality rate (*m*) and the lower (LCL) and upper (UCL) confidence limits (95%) of each offspring size class of the first census (1996): small (< 15 cm tall), medium (individuals from 15 to 50 cm tall) and large (>50 cm tall) individuals. Mean from 1996 to 1999. The mean (± standard deviation) numbers of offspring were 126 (± 58) of small, 78 (± 16) of medium and 16 (± 3) of large individuals. Mortality rate and confidence limits suffered arcsine retransformation. There was no overlay between the confidence limits of small individuals with the confidence limits of medium and large individuals, while there was overlay between the confidence limits of medium and large individuals.

	Small	**Medium**	**Large**
m (%)	48.8	16.7	16.2
LCL	36.5	8.9	4.4
UCL	64.3	29.0	33.7

Table 2: Mean (± SD) number of *E. glaziovii* fruit (Fruit) and the proportion between the fruit number under and out of the parental tree and between plots with high and low conspecific fruit density (Proportion). The mean (± SD) number of recruitment of new small individuals in each place (Recruitment), and the expected number of recruitment under and out of the parental tree and between plots with high and low conspecific fruit density (Expected). The expected recruitment was obtained by the mean number of fruit sampled. In addition, the number of observed recruitment was the mean of new small individuals sampled from 1996 to 1999. The mean number of fruit, in its turn, was calculated from samples made in 1998 and 1999.

	Fruit	**Proportion**	**Recruitment**	**Expected**
Under	801 (± 180)	0.75	28 (± 15)	32
Out	270 (± 200)	0.25	15 (± 11)	11
High	1035 (± 376)	0.95	38 (± 25)	41
Low	55 (± 56)	0.05	5 (± 1)	2

Table 3: Annual mortality rate (*m*) and the lower (LSD) and upper (USD) standard deviation of *E. glaziovii* offspring under and out of the parental crown; and in plots with high and low conspecific offspring density. Mean from 1996 to 1999. The mean (± standard deviation) numbers of offspring were 126 (± 20) under, 97 (± 7) out of the parental crown, and 176 (± 15) in high and 44 (± 14) in low density plots. Mortality rate and confidence limits suffered arcsine retransformation. There was no overlay between the confidence limits under and out of the parental crown and between plots with high and low density of conspecific offspring

	Under	**Out**	**High**	**Low**
m (%)	15.1	8.9	12.1	10.0
LSD	10.6	5.6	9.3	5.1
USD	22.8	14.5	16.0	17.8

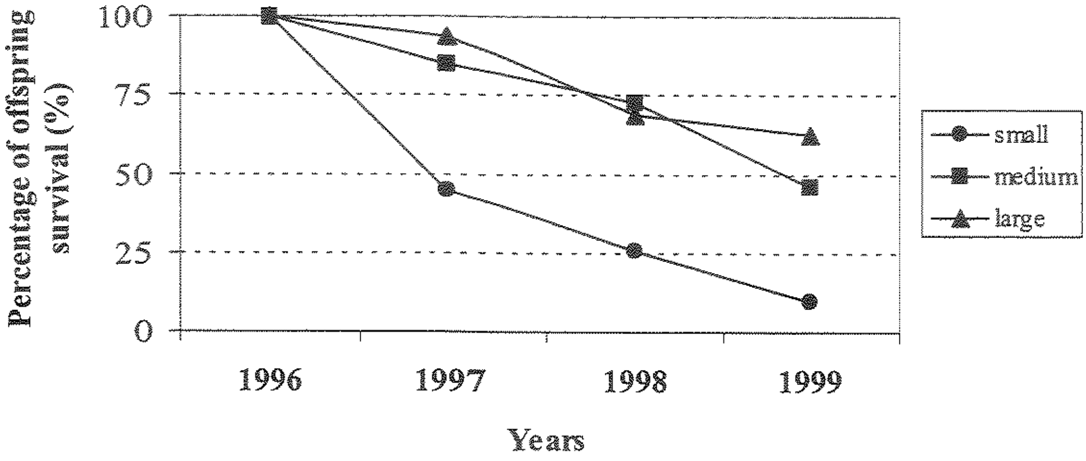

Figure 1: Survivorship curves of small (n=202), medium (n=59) and large (n=16) individuals of *E. glaziovii* of the first year census (1996) along the time.

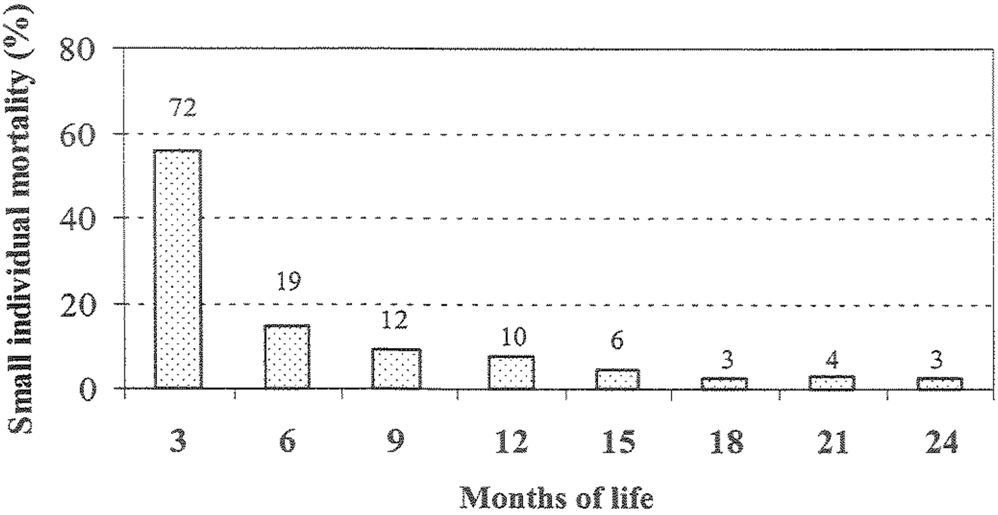

Figure 2: Percentage (%) of the small individual's mortality at every three months of life, and their sample size on the bars.

CONSIDERAÇÕES FINAIS

O escape da semente de dentro do fruto é provavelmente uma das etapas da regeneração de *E. glaziovii* mais críticas, pois foram encontradas várias sementes podres e outras já embebidas dentro dos frutos (Ramos & Andrade dados não publicados). Este fato pode indicar que as sementes estão com dificuldade de sair dos frutos, varias delas ficam embebidas lá dentro, e como o fruto é muito duro e a radícula não consegue penetra-lo, a maioria delas acabam perecendo e apodrecendo dentro deles. Provavelmente essa dificuldade apresentada é conseqüência da diminuição da população de dispersores das suas sementes pela caça ilegal nas áreas estudadas. Os prováveis dispersores de *E. glaziovii,* baseado em informações para outras espécies do gênero (Janzen 1981a,b; 1982a,b,c) e baseado nos dispersores das espécies com frutos semelhantes e presente em sua área de distribuição, devem ser antas (*Tapirus terrestris*), cutias (*Dasiprocta leporina.*), catetos (*Tayassu tajacu*) e queixadas (*Tayassu pecari*). Essas espécies, por sua vez, são muito visadas por caçadores ilegais e suas populações tendem a se reduzir em áreas fragmentadas e/ou com grande pressão de caça (Chiarello 1999). Tanto o Parque Nacional da Floresta da Tijuca que é um parque urbano, quanto a Reserva Biológica de Poço das Antas sofrem muita pressão de caçadores e seus órgãos de fiscalização possuem poucas condições humanas, materiais e monetárias para controlar ou diminuir essa pressão (IBAMA com. pess.).

Mas mesmo com a população de dispersores ausente ou reduzida, a regeneração dessa espécie parece estar ocorrendo. As sementes que conseguem sair de dentro dos frutos são capazes de germinar e crescer ao redor do adulto, em um ambiente pouco iluminado. Porém, a inclinação influencia a distribuição espacial tanto dos frutos como dos jovens de

E. glaziovii. Porém, provavelmente se os seus dispersores continuarem com suas populações reduzidas nestas áreas, essa população de *E. glaziovii* irá a longo prazo sair dos terrenos inclinados atingindo terrenos planos, e poderá desaparecer se não forem capazes de competir com as espécies presentes neste ambiente.

De acordo com Forget (1992) dispersores secundários, como roedores, podem distribuir mais homogeneamente as sementes de árvores que se localizam em terrenos inclinados. Segundo este autor, a dispersão secundária para a subida do terreno (terreno acima da arvore parental) pode compensar o efeito da inclinação que influencia o deslocamento das sementes para a descida do terreno (terreno abaixo da arvore parental). Mas para verificar este fato, é preciso um estudo específico sobre dispersão de sementes ou remoção de frutos. Seria interessante se fosse possível comparar com outras áreas que possuam uma população mais protegida desses potenciais dispersores de *E. glaziovii*, como a Reserva da Companhia do Vale do Rio Doce em Linhares, Espírito Santo (Chiarello 1999).

Os adultos de *E. glaziovii* são esparsamente distribuídos nas florestas, com os indivíduos muito longe um dos outros. Os frutos e jovens desta espécie estão agregados embaixo da copa da planta parental. Por sua vez, o recrutamento de novos indivíduos e a sobrevivência dos jovens não estão sendo influenciados embaixo da copa da planta parental nem pela densidade de jovens coespecíficos. Portanto, parece que os processos ocorrendo na escala espacial e temporal estudada, não explicam a baixa densidade dos adultos dessa espécie. Provavelmente os processos que explicam esse padrão espacial dos adultos podem estar ocorrendo em uma maior escala espacial e temporal. Pode ser que a regeneração ao redor dos adultos seja importante apenas para a substituição dos mesmos se eles morrerem. Essa espécie pode requerer sítios específicos para conseguir germinar e se estabelecer, e a colonização de novos sítios a partir dos adulto pré estabelecidos, pode depender da dispersão à longa distância de alguma de suas semente a esses sítios. Essa dispersão de longo alcance, no entanto, pode ocorrer apenas em intervalos de tempos muito grandes ou em condições muito especiais. Portanto pode ser que a distribuição espacial dos adultos de *E. glaziovii* seja influenciada pela distribuição de micrositios favoráveis (que devem ser esparsamente distribuídos) e pela chance de uma de suas sementes chegar a esses locais favoráveis.

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