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Spatial Heterogeneity and its Influence on *Copaifera langsdorffii* Desf. (Caesalpiniaceae)

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ABSTRACT

Population dynamics and structure of young individuals of the tree Copaifera langsdorffii *Desf. (Caesalpiniaceae) were studied in the gallery forest of the Panga Ecological Station, Uberlândia, MG, Brazil. Three distinct habitats were recognized in this forest, Dike, Middle and Edge zone. Four annual surveys of plant height, diameter at plant base and density were made between 1993 and 1996. The species showed an aggregated distribution in all three habitats. Population structure in all four surveys presented the typical reversed "J" form, characteristic of populations in local regeneration. For the whole population, mortality rates during the four years were constant and low (average of 4.8 % per year), while recruitment declined during the same period (average of 2.9 % per year). The* C. langsdorffii *seedling and sapling intraspecific density had a negative effect on growth, possibly due to the action of herbivores and pathogens.*

Key words: Gallery forest; seedling; recruitment, mortality, growth, saplings

INTRODUCTION

Gallery forests follow streams and drainage lines in the savannas of Central Brazil. They grow on hydromorphic soils, have different degrees of deciduousness and may appear along one or both margins of the watercourse (Mantovani, 1989). Most gallery forests are subject to periodic flooding. Overbank flooding is common in the rain season, when large rain events cause an increase of flux of water. The topography (depression in some places), the soil feature (hydromorphic soil) and water table fluctuations cause a second type and more durable flooding effect, during the entire rainy season, this prolonged flooding and its effect is explored in this work. The light conditions associated with different susceptibility to flooding determine different habitat types in the gallery forests (Schiavini, 1992). Due to these particular characteristics, gallery forests are useful models to study spatial heterogeneity in the environment and the influence of this heterogeneity on population structure and dynamics of forest communities (Schiavini, 1992; Oliveira - Filho et al., 1994). How natural plant populations seem to be regulated by density dependent processes (Antonovics and Levin, 1980; Crawley, 1990; Condit et al., 1994) in association with environmental heterogeneity in space and time (Fowler, 1988), gallery forests could be used to test hypotheses of populations regulation.

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Studies of density and its effects have been limited to the direct interference between intraspecific neighbors (Mithen et al., 1984) through limitation of resources such as light or nutrients (Berntson and Wayne, 2000). However, low density tree populations in tropical forests is common, and neighbors are seldom conspecifics. Density dependent processes may be detected mainly by increase in density of natural enemies. However, intraspecific density dependent processes are difficult to detect in field conditions, since environmental heterogeneity obscures these effects. One way to circumvent this difficulty is to measure performance (mortality, growth and recruitment) of individual plants under different environmental conditions (Condit et al., 1994).

Spatial distribution is an important demographic component as it reflects several factors such as parental distribution, seed dispersal, predation and herbivory, and the distribution of safe-sites (Hutchings, 1986). The association of periodic flooding, with either intolerance or tolerance flooding may determine the distribution of plants in gallery forests. The increase of light to the forest floor, mainly at the edge (adjacent to the savanna), associated with flood may determine the availability of safe-sites, and in turn the plant establishment and growth. Spatial distribution of gallery forests tree species between habitats and within habitats should reflect the distribution of these safe-sites.

We studied the effect of flooding and light conditions in spatial distribution, size structure, growth rates, recruitment and mortality of seedlings and saplings of *Copaifera langsdorffii* Desf., a late successional, flood intolerant, common and widespread tree. We assumed as our hypotheses: 1 – the distribution of *C. langsdorffii* seedlings and saplings was clumped on the dry areas (less prone to flooding); 2 – the growth of seedlings and saplings of *C. langsdorffii* was directly related to canopy cover; 3 – the density of intraspecific seedlings and saplings was negatively related to growth; 4 – The mortality rates of seedlings and saplings could be higher in the flooded habitat.

MATERIAL AND METHODS

Species description and study site: Copaifera langsdorffii (Caesalpiniaceae) is a typical gallery forest tree that may also occur in adjacent savanna communities (Cerrado) in Central Brazil. It can reach 25 m in height in the forest (it is smaller in the savanna). Seeds have an aril and are dispersed through animals, particularly by birds. Their seedlings do not survive prolonged floods (2 to 7 days to die) (Barbosa et al., 1992). Topography and soil characteristics result in different degrees of flooding in the forest. Three habitats were recognized, associated with the nature and duration of the flooding, soil features, light conditions and floristic composition (Schiavini, 1992): 1) Dike: a 10 m wide zone near the watercourse, which was characterized by deposition of alluvial sandy sediments, and was less prone to periodic flooding. 2) Middle: the depression after the Dike that was roughly parallel to the watercourse, with hydromorphic soil; it was more prone to periodic flooding. 3) Edge: the boundary zone adjacent to the open savanna, characterized by moderate hydromorphic soil and higher incident light than the other habitats. The plant community of gallery forests included species that were tolerant and intolerant to the periodic flooding (Schiavini, 1992; Walter, 1995).

Seedlings and saplings of *C. langsdorffii* were sampled at the Panga Ecological Station located in Uberlândia, Minas Gerais, Brazil. The station has a total area of 400 ha and comprises several vegetation types including forests, cerrado grasslands and woodlands (Fig. 1). The regional climate is of Aw type (Köppen) with dry winters (from May through September) and rainy summers (from October to April). The average annual precipitation is 1500 mm. The studied area was 10,000 m^2 of forest. The gallery forest forms a continuous forest along the river. The sample area was 3,000 m^2, divided into 120 plots of 5 x 5 m. Forty plots were allocated for each habitat, the Dike, Middle and the Edge (Fig. 1). Annual surveys were conducted in 1993, 1994, 1995 and 1996. For each survey, all plants of *C. langsdorffii* in each of the 120 plots were individually tagged, measured for height and diameter at base.

Demography and Spatial distribution: All seedlings and saplings of *C. langsdorffii* found in the 120 plots were mapped. Their pattern of spatial distribution in each habitat was described by comparing the 1993 survey, using the index of dispersion:

$$ID = \frac{s^2}{x}$$

where: s^2 = variance
x = mean

and Green's index (Ludwig and Reynolds, 1988):

$$GI = \frac{(s^2/x) - 1}{N - 1}$$

where: s^2 = variance
x = mean
N = number of individuals.

We found a different N of seedling and sapling between the habitats types. The index of dispersion is dependent on sample size, since Green's index is more appropriate for comparisons of the degree of clustering (Ludwig and Reynolds, 1988).

Size classes were determined using the relation A/k, where A was the amplitude and k was Sturges algorithm, 1+ 3.3log N, N being the number of individuals (Gerardi and Silva, 1981). The Komolgorov - Smirnov test compared the differences between the 1993 and 1996 frequencies in the size structure curves.

Differences in mortality and recruitment between surveys and habitat types (Dike, Middle and Edge) were tested using chi-square.

The influence of habitat, canopy cover and density on growth: Growth was estimated using the final/initial height ratio or the final/initial diameter ratio. This allowed us to compare differences in growth between size classes and habitats. Differences were tested with the Kruskal - Wallis test (Sokal and Rohlf, 1981). The influence of cover on growth was examined using canopy pictures of each plot. The pictures were taken with black and white 35 mm film, iso 400, with a SLR camera fitted with a 35 mm wide - angle lens. The diaphragm was set for sub-exposition, in order to maximize the contrast between light and dark areas in the pictures. One picture was taken in the center of each plot, at 55 cm above ground. Data collection took 15 days in July 1996, between 10 a.m. and 2 p.m.. The pictures were digitized using a scanner (200 - dpi resolution); dark and white areas were quantified to calculate a relative index of canopy cover. The relationship between canopy cover index and growth of plants of *C. langsdorffii* was tested using the Spearman Rank Order Correlation. Density of seedlings and saplings of *C. langsdorffii* in the plots was also correlated with growth by the Spearman Rank test.

RESULTS

The total number of seedlings and saplings of *C. langsdorffii* decreased from 481 in 1993 to 454 in 1996, the mean density of seedlings and saplings was 0.16 and 0.15 individuals/m^2, respectively. There was a clear concentration of seedlings and saplings on the Dike, corresponding to an average of 61 % of all plants sampled during the four years. The Middle had 21.5 % and the Edge 17.5 % of the plants. Both the dispersion coefficient and Green's index indicated an aggregated distribution for the three gallery forest habitats (Table 1). The flooded habitat (Middle) presented a higher degree of cluster than the Dike and Edge.

Table 1 - Dispersion and Green's index of individuals of *Copaifera langsdorffii* in the three habitats of a gallery forest in Panga Ecological Station for the 1993 and 1996 surveys. Values for three microhabitats of gallery forest. All values of dispersion index are significantly different from 1 at 5 % level in the chi-square test. ID = Index of Dispersion, GI = Green's Index.

Habitat	1993		1996	
	ID	GI	ID	GI
Dike	4.77	0.0133	5.12	0.0149
Middle	8.19	0.0672	5.81	0.0506
Edge	2.88	0.0229	2.43	0.0183

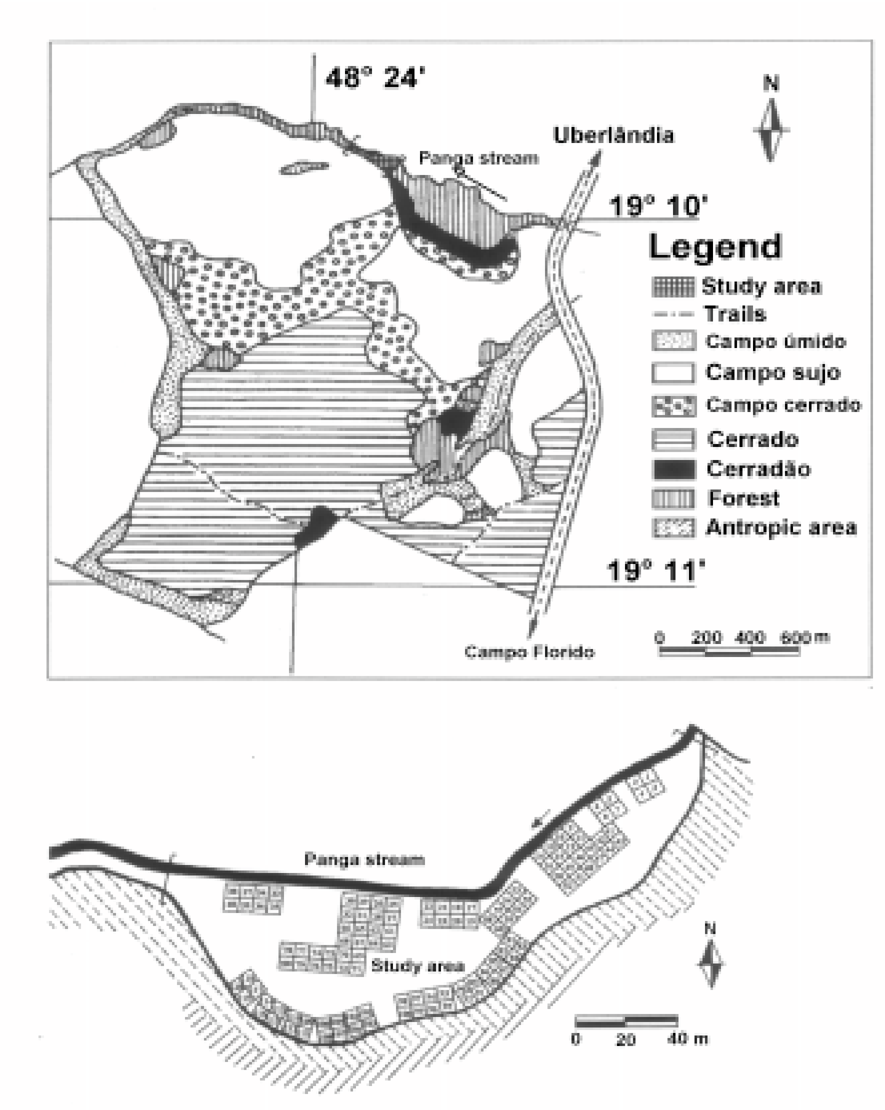


Figure 1 - Map of the plant communities in Panga Ecological Station, below study area with plot location, Uberlândia, Minas Gerais, Brazil (Adapted from Schiavini, 1992).

No significant difference in mortality (P = 0.08) and recruitment (P = 0.37) was found between habitats, but mortality was significantly higher than recruitment during the four year period (P < 0.005). Recruitment decreased over time, while mortality remained constant (Table 2).

Mortality was concentrated in the first three diameter classes, of the 69 plants that died during the study period, 60 were in the smallest size class (diameter between 1 - 3.3 mm).

Size frequency distribution followed a typical reversed "J", for both height and diameter, with a high concentration of plants in the first class (Fig. 2). The Kolmogorov - Smirnov test showed a significant difference between the 1993 and the 1996 surveys for height in the Edge Habitat (P < 0.001) (data not presented) and for diameter in the Dike Habitat (P < 0.01) (Fig. 2 B), Edge Habitat (P < 0.004) (Fig. 2 D) and for the total population (P < 0.001) (Fig. 2 A). The modification of size classes between years was caused by concentrated mortality in the first three classes associated with low recruitment during the period.

There was highly significant difference in growth between habitats to the seedlings and saplings of *C. langsdorffii* (Fig. 3). Plants in the Edge had a larger growth ratio than plants in the Dike and the Middle Habitat for height (P < 0.001) and diameter (P < 0.001). Growth differed also between diameter classes (P < 0.01). The first diameter class had the highest growth ratio and there was a tendency reducing growth ratio on the larger diameters (data not presented). There was relationship between canopy cover and growth ratio (Table 3). A significant correlation was found between diameter growth ratio and canopy cover in the Middle habitat (r = 0.533, P < 0.01 in Spearman Correlation). Low correlation also occurred between growth ratio of seedling and saplings of *C. langsdorffii* and plot density of conspecifics. A significant negative correlation was found between diameter growth ratio to all seedlings and saplings and density of conspecifcs plot density (r = -0.2, P = 0.04 in Spearman Correlation).

Table 2 - Spearman Rank Order Correlation between growth ratio and canopy cover, for *Copaifera langsdorffii* in the Panga Ecological Station. (*) Indicates significant difference at the 5 % level.

Habitat	**Growth ratio X Canopy cover**	
	Height	**Diameter**
Dike	-0.236	-0.003
Middle	0.071	0.533*
Edge	0.202	0.033
Total Population	-0,003	0.134

DISCUSSION

The most important determinant of tree spatial distribution in gallery forest seems to be the periodic flooding and the species tolerance to this condition (Walter, 1995). Adult individuals of *C. langsdorffii* have been restricted to areas not subjected to flooding, which led some authors to classify the species as intolerant to flooding (Schiavini, 1992; Walter, 1995). In this study, we observed that seedlings and saplings of *C. langsdorffii* were found mainly in the driest habitat (the Dike). The spatial distribution of saplings and seedlings seems to reflect the flooding conditions found in each habitat.

The Dike population had the smallest degree of clumping, possibly due to its dry sandy soil and microtopographic characteristics, which prevented prolonged inundation (Schiavini, 1992). The Middle population had the highest degree of clumping. This habitat has hydromorphic soil and is characterized by a depression that suffers periodic and prolonged flooding (Schiavini, 1992). Distribution of *C. langsdorffii* in the Middle is limited to areas where alluvial sediment deposition creates small mounds (personal observation). The presence of these mounds modified germination rate and seedling survival, as has been shown in studies of other floodplain systems (Jones et al., 1994), possibly influencing *C. langsdorffii* distribution. The Edge population showed an intermediate degree of clumping and this habitats been influenced by indirect light from the open savanna (Schiavini, 1992).

Survival and recruitment were similar and could not explain the high differences in abundance between habitats. The factors determining distribution probably acted during seed dispersal and seedling establishment. Parent plants were concentrated on the Dike (Schiavini, 1992), and probably contributed a larger input of seeds to this habitat than the others, which would increase establishment. After dispersion, the density of seeds was higher near the parent plant and decreased with distance (Janzen, 1970; Whitmore, 1988). The association between spatial and temporal heterogeneity brought about by water level fluctuations, erosion and sedimentation might create differential site suitability between habitats for seedling establishment (Bertoni and Martins, 1987).

Table 3 - Mortality and recruitment of seedlings and saplings of *Copaifera langsdorffii* in the gallery forest of Panga Ecological Station between 1993 and 1996 surveys. mort = mortality; recr = recruitment.

Habitat	**93-94**		**94-95**		**95-96**		**Annual (%)**	**average**
	mort	recr	mort	recr	mort	Recr	mort	Recr
Dike	14 (4.8%)	20 (6.9%)	12 (4.1%)	7 (2.4%)	13 (4.5%)	2(0.7%)	4.5	3.5
Middle	10 (9.2%)	4 (3.7%)	7 (6.8%)	4 (3.9%)	5 (5.0%)	1 (1.0%)	6.8	2.8
Edge	2 (2.4%)	3 (3.6%)	1 (1.2%)	1 (1.2%)	5 (6.5%)	0 (0.0%)	3.2	1.6
Total	26 (5.4%)	27 (5.6%)	20 (4.1%)	12 (2.5%)	23 (4.8%)	3 (0.6%)	4.8	2.9

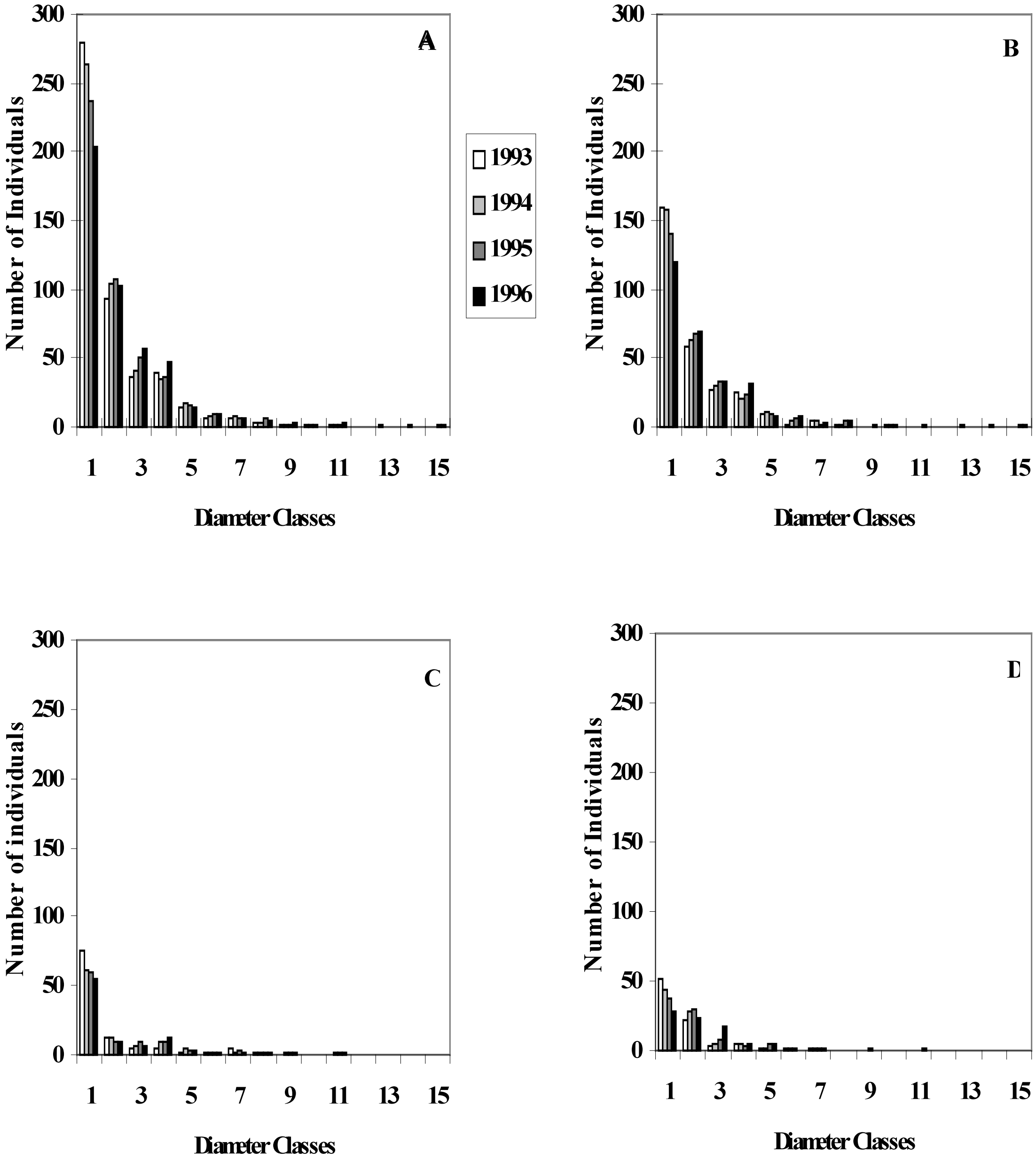
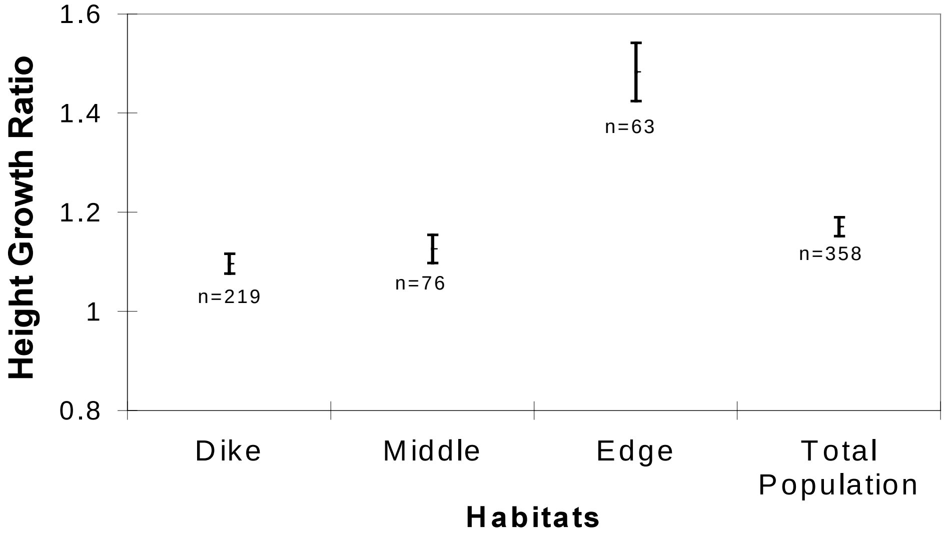


Figure 2 - Diameter frequency distribution of *Copaifera langsdorffii* for Total population (A), Dike (B), Middle (C) and Edge (D) of a gallery forest in the Panga Ecological Station. Diameter class in mm, **1**: 1 - 3,29; **2**: 3,3 - 5,59; **3**: 5,6 - 7,89; **4**: 7,9 - 10,19; **5**: 10,20 - 12,49; **6**: 12,50 - 14,79; **7**: 14,80 - 17,09; **8**: 17,10 - 19,39; **9**: 19,40 - 21,69; **10**: 21,70 - 23.99; **11**: 24 - 26,29; **12**: 26,30 - 28,59; **13**: 28,60 - 30,89; **14**: 30,90 - 33,19; **15**: 33,20 - 35,50.



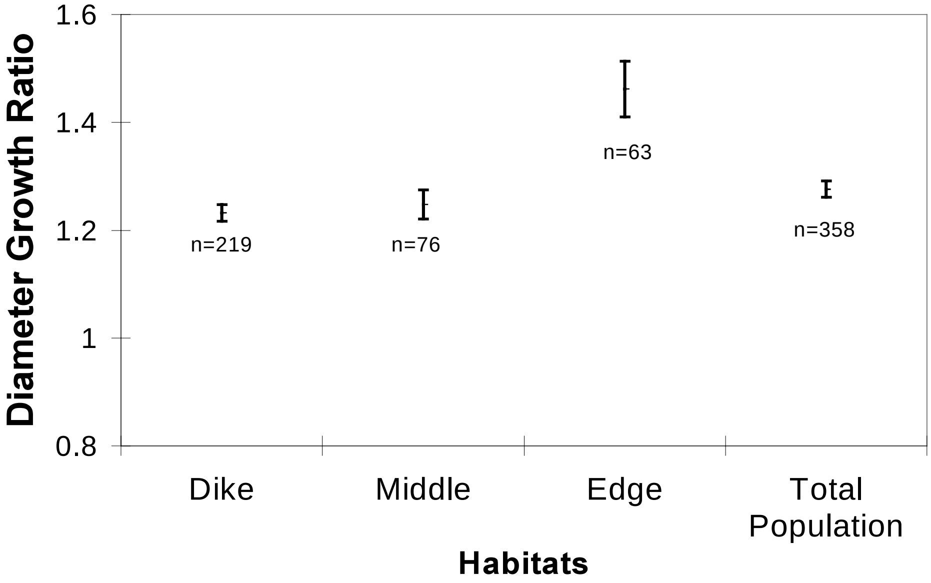


Figure 3 - Growth ratios of seedlings and saplings of *Copaifera langsdorffii* for the three habitats and total population. Growth was measured as the ratio between final size (1996 survey) and initial size (1993 survey) as measured by both height and diameter. Means with one standard error.

In undisturbed forests, tree losses are continuously replaced by new recruits in “steady-state” populations (Swaine et al., 1987), even though constant recruitment and mortality rates, commonly used in population dynamics’ models are probably unrealistic (Crawley, 1990), as has been the case of *C. langsdorffii*.

During the study period, the mortality was higher than recruitment because adult trees did not produce seeds in the area (personal observation). *C. langsdorffii* usually produced seeds at three-year intervals (Leite and Salomão, 1992). It has been reported that in tropical forests recruitment varied from years of large seed production (mast years) to years of low seed production and recruitment (De Steven, 1994).

In tropical forests, mortality varied within local sites and between successive periods (Swaine et al., 1987), even though this was not true for *C. langsdorffii* during the duration of this study. Seedling and sapling mortality was similar between habitats and possibly caused by similar agents, such as resource limitation and inter and intraspecific competition. Catastrophic events such as “drought” were not the main mortality factor in this tree population as been reported in other studies (Condit et al., 1995), since no large fluctuations in population size were seen. In the absence of catastrophic mortality, population fluctuations should follow years of high seed production, when recruitment rates are expected to be higher than in subsequent years. Thus, fluctuations in the population of *C. langsdorffii* should be directly linked to its multi-annual reproductive cycle, a pattern reported by De Steven (1994) for tropical trees in which high recruitment rates were a consequence of increased input of seeds, followed by declines caused by mortality and low seed production and low recruitment.

The relatively higher growth found in the Edge habitat could be related to the high mortality rate of the Edge pioneer tree *Miconia thaezans* (80 % of the mature plants have died in the last five years - Schiavini, unpublished data). This species forms dense clumps, but mature trees suffer high mortality and form gaps in the canopy. Seedlings and saplings of *C. langsdorffii* could have benefited from the low competitive influence and consequently had higher growth than in the other habitats, a response also seen for other tropical tree species in canopy gaps (Denslow, 1987; Martinez-Ramos et al., 1988; Whitmore, 1988; De Steven, 1994; Forget, 1994).

Canopy cover was not the only factor affecting growth in *C. langsdorffii*, as suggested by the low relationship found between growth and cover index. Specific site conditions such as number and size of neighbors, soil fertility, grazing, and genetic variability might have influenced the results. Conspecific neighbors may alter the growth of plants by depleting limited resources, by producing toxins and by influencing the behavior of natural enemies (Harper, 1977). Studies of intraspecific density dependent effects usually take into consideration the direct effects of competition for light and nutrients that are important factors on intraspecific competition (Liddle et al., 1982, Mithen et al., 1984; Weiner and Thomas, 1986), but often they do not consider the effect of increase in concentration of natural enemies (Janzen, 1970; Isaacs et al., 1996) and herbivory (Angulo-Sandoval and Aide, 2000; Silva Matos, 2000). Since the population density of seedling and saplings of *C. langsdorffii* was low, usually 1 plant/m^2 in the densest plots, the intraspecific density effect on growth of this tropical tree would be minimal and be related more to the concentration of natural enemies. Grazing and fungal attacks have been observed, but not quantified in the field (personal observation). Even at low intraspecific densities a negative effect of density, due to concentration of natural enemies, may occur in tropical trees (Condit et al., 1994).

Structured populations with ample longevity of their individuals and repeated, sometimes yearly, recruitment have age differences between plants which are the main causes of height distributions (Weiner, 1988). The reversed “J” curve of size distributions has been found for several tropical trees in Brazil and indicated a consistent recruitment and growth of populations (Leite and Salomão, 1992; Schiavini, 1992). Despite other possible marginal causes of the reversed “J” curve, the data presented here suggests that *C. langsdorffii* presented local regeneration.

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RESUMO

A estrutura e a dinâmica dos indivíduos jovens da espécie *Copaifera langsdorffii* Desf. (Caesapiniaceae) foi estudada na mata de galeria da Estação Ecológica do Panga (Uberlândia, MG - Brasil). A mata de galeria neste estudo foi descrita como apresentando 3 ambientes: Dique, Meio e Borda. O trabalho de campo consistiu de quatro levantamentos, realizados anualmente entre 1993 e 1996. A população foi caracterizada como agrupada nos três ambientes. A estrutura de tamanho da população se apresentou como uma curva em “J” invertido, indicando regeneração local. As taxas de mortalidade foram constantes e baixas durante os quatro anos (4,8 % por ano), já as de recrutamento sofreram um declínio durante o mesmo período (2,9 % por ano). A densidade intraespecífica das plântulas e indivíduos jovens de *C. langsdorffii* tem um efeito negativo nas taxas de crescimento, possivelmente devido a ação de herbívoros e patógenos.

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