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ORIGINAL ARTICLE

Natural regeneration dynamics of *Couratari guianensis* in a tropical forest selectively logged in Moju, state of Para, Brazil

Dinâmica da regeneração natural de Couratari guianensis em floresta tropical explorada seletivamente, Moju-PA

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ABSTRACT: Studies on natural regeneration of timber tree species are of great scientific interest because they are essential for the proper development and implementation of management plans and silvicultural treatments, allowing sustainable use of forest resources. This study aimed to evaluate the population dynamics of *Couratari guianensis* Aubl., Family Lecythidaceae, a wood species known as tauari, in a terra firme tropical rain forest, selectively exploited in Moju, state of Pará, Brazil, over 12 years after harvesting, which originated gaps with sizes ranging between 231 and 748 m^2, of which nine were used in the study. The center of each gap was determined and four transects of 10 × 50 m were marked in the North, South, East and West directions. In order to evaluate natural regeneration, three 2 × 2 m plots were implanted on each transect at the distances of 20 and 40 m off the edge. We used the mathematical models Natural Regeneration Rate (RR%), Recruitment (R%) and Mortality (M%) for the study of natural dynamics. Data were analyzed in the BioStat software by analysis of variance on three factors (center and directions, forest gap size class and study period). No significant differences were found in RR%, R% and M% values regarding the three factors. In general, *Couratari guianensis* Aubl. behaves as an intermediate plant species in terms of demand for light.

RESUMO: *Estudos sobre a regeneração natural de espécies arbóreas madeireiras são de grande interesse científico por serem essenciais para a elaboração e a aplicação correta dos planos de manejo e dos tratamentos silviculturais, permitindo um aproveitamento sustentável dos recursos florestais. O objetivo deste trabalho foi avaliar a dinâmica populacional de Couratari guianensis Aubl., Família Lecythidaceae, uma espécie madeireira conhecida como tauari, em uma floresta tropical úmida de terra firme, explorada seletivamente em Moju-PA, ao longo de 12 anos após a colheita, da qual se originaram clareiras com tamanhos que variaram entre 231 e 748 metros quadrados, dentre as quais, nove foram utilizadas neste estudo. Cada clareira teve seu centro determinado e, a partir da borda, foram marcadas quatro faixas de 10 × 50 m nas direções Norte, Sul, Leste e Oeste. Para a avaliação da regeneração natural, foram implantadas três parcelas de 2 × 2 m em cada faixa, nas distâncias de borda de 20 e 40 m. Para o estudo da dinâmica, utilizaram-se os modelos matemáticos denominados Taxa de Regeneração Natural (TR%), Ingresso (I%) e Mortalidade (M%). Os dados foram analisados no programa Bioestat por meio da análise de variância de três fatores (centro e direções, classes de tamanho das clareiras e período de estudo), não havendo diferença significativa nos valores de regeneração natural em função dos três fatores. O mesmo aconteceu com ingresso e mortalidade. De um modo geral, Couratari guianensis Aubl. comporta-se como espécie intermediária em termos de demanda por luz.*

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1 Introduction

In recent years, the Amazon has received special attention because it is the most diverse area of tropical forest worldwide, home to at least 40,000 plant, 427 mammal, 1294 bird, 378 reptile and approximately 3,000 fish species (SILVA; RYLANDS; FONSECA, 2005). The great biodiversity of the Amazon biome holds a huge economic potential. However, its resources of timber and non-timber products are still being exploited irrationally because unplanned logging is prevalent in the region. The heterogeneity of tropical forests and their complex structure and dynamics hinder their sustainable exploitation due to lack of knowledge. This information is the main tool used by silviculturists to assess the potential of these resources and define the strategies for their management. Although forest management is the most appropriate form recommended for the utilization of these natural resources on a sustainable basis, it is worth noting that most natural forest-based products in the market are not from managed forests.

In this context, the study of rain forest dynamics is essential to support decision-making when selecting the best silvicultural system to regenerate forests. Regeneration development is the basis to forest dynamics maintenance, which is stimulated primarily by increased light intensity after gap formation. This fact shows the positive or negative influence of light on vegetation behavior.

Regeneration is part of the cycle of forest growth and refers to the initial stages of its establishment and development. It is a set of young individuals that will be recruited to perpetuate populations of species and forest ecosystems. The guarantee of permanence of a certain species in a forest is directly related to the number of individuals and their distribution in diameter classes.

Young plants of species of more advanced stages of succession grow in environments of lower light availability and the impacts resulting from changes in this environment, such as the opening of forest gaps, may bring harmful consequences to these plants because sudden exposure to high irradiance may cause photoinhibition or permanent damage to their photosynthetic apparatus (GONÇALVES et al., 2010). In very large gaps, established plantlets and seedlings may experience small growth or even die due to high radiation load (WHITMORE, 1978). It must be considered, however, that there are several factors that influence the growth differences between species. The demand for light and regeneration strategy of plant species are related to potential growth rate (FINEGAN; CAMACHO, 1999). Phytosociology in communities also influences this behavior as the size that a tree can reach at a certain age depends on the space available for its growth (WADSWORTH, 2000).

Rain forests are characterized by a large amount of species with varied growth rates and any dichotomic classification into ecologic groups, such as climax/pioneer, will always result in a large number of species that do not fit in any of the groups. According Whitmore (1984), there is a continuous gradient of demand for light in forest species that interacts with gap sizes, recovering time and their causes along succession. In addition, there are differences in species growth patterns regarding height and diameter, whose reasons are associated with physiological time, which varies according to the species and their stage of development (TONINI; OLIVEIRA JUNIOR; SCHWENGBER, 2008).

In this context, forest management for timber production presents implications to natural regeneration, some with opposing effects. On the one hand, there are damages and mortality of individuals, considerable reduction in fruit production and increased light availability in the remaining forest; on the other hand, there is the influence in the spatial distribution of species, with changes in spatial distribution of the natural regeneration of harvested and remaining species. The integrated impact of these effects can be evaluated only a few years after forest harvesting, but studies on the effect of logging on the natural regeneration of some species have only been performed soon after harvest (GOMEZ, 2011). *Couratari guianensis* is a group composed of several species of Lecythidaceae timber known as tauari, grouped by their technological characteristics. Among the tauari species, *C. guianensis* presents the largest area of continuous distribution covering almost all the Amazon biome, reaching Costa Rica, but always with low densities. Because it is the only one that coexists with all other tauari species in the Amazon, it has been suggested that it present high phenotypic plasticity (PROCÓPIO et al., 2010).

There are no studies on the population dynamics of *C. guianensis* in the literature. Likewise, studies related to survival and mortality of tree species in managed forests are scarce and show contrasting results between highly shade-tolerant and shade-intolerant species (BLOOR; GRUBB, 2003). Nevertheless, it is crucial for tropical forestry to know the rates of recruitment, mortality and growth that determine the regenerative capacity of timber species through the monitoring of managed forests.

Understanding the individual behavior of forest species regarding changes in the light environment provides reliable information to identify its specific vulnerability and ensure conservation and sustainable forest management.In this study, we aimed to evaluate the population dynamics of *Couratari guianensis* concerning its recruitment, mortality and natural regeneration capacity rates according to center and directions, forest gap size class and study period.

2 Materials and Methods

The study was carried out in the Experimental Field of "Embrapa Amazônia Oriental" located at km 30, Rodovia PA 150, in the microregion of Tomé-Açu, state of Para, Brazil. This field is located between the following geographic coordinates: 2º 08' and 2° 12' latitude south; 48° 47' and 48º 48' longitude west of Greenwich meridian. The total area covers 1095 ha from which a 200 ha site that underwent low impact logging was selected. According to Köppen classification, the area presents Ami climate with annual average temperature ranging from 25 to 27 °C, monthly insolation from 148.0 to 275.8 h, air relative humidity of approximately 85% and annual rainfall in 2000 of 3000 mm with the rainiest period from January to June. It presents flat to gently undulating relief with small unevenness ranging from zero to 3% and predominantly well drained soils classified as typical Yellow Latosol and Yellow

Argisol (SANTOS et al., 1985).The vegetation is classified as Dense Rain Forest (VELOSO; RANGEL FILHO; LIMA, 1991) with large tree species, 25-30 m in height. Low impact logging was performed in the selected 200 ha site in accordance with the forestry legislation in force between October and November 1997. According to Lopes et al. (2001), 24 tree species were collected in the area, among which *Newtonia suaveolens* (Micah) Brenan, *Vouacapoua American* Aubl. and *Manilkara huberi* Standl. stood out because of their large volumes.

Nine gaps created by the 1997 logging ranging from 231 to 748 m^2, averaging 497 m^2 were selected; they were classified by the area as small (231-340 m^2), medium (437-600 m^2) and large (666-748 m^2).

In each of the nine gaps, 2 × 2 m plots were implemented in the center and on the edge, as well as on transects at 20 and 40 m off the edge in the North, South, East and West directions (Figure 1). In these plots, all *Couratari guianensis* individuals with total height (TH) ≥ 10 cm and diameter at breast height (DBH) < 5 cm were identified and measured. Botanical material was collected to confirm identification with the herbarium 'IAN - Embrapa Amazônia Oriental' and the museum 'Museu Paraense Emílio Göeldi'.

We conducted a quarterly monitoring from March 1998 to March 2001, totaling 13 surveys, and two measurements in March and October 2007 and one in March 2010, amounting to 16 measurements. However, in this study, in the 1998-2001 period, annual measuring intervals are considered and the study periods were analyzed as follows: Year 1 (1998-1999), Year 2 (1998-2000), Year 3 (1998-2001), Year 9.5 (1998-2007), and Year 12 (1998-2010).

C. guianensis behavior was assessed by the natural regeneration rate (RR), equation modified by Mory and Jardim (2001), defined as the ratio between the absolute abundance resulted from the dynamic process of natural regeneration (recruitment, growth and mortality) and the absolute abundance at the beginning of the study, expressed in percentage and represented by the following equation: $RR = [(A_1 - A_0)/(A_1 + A_0)].100$, where:

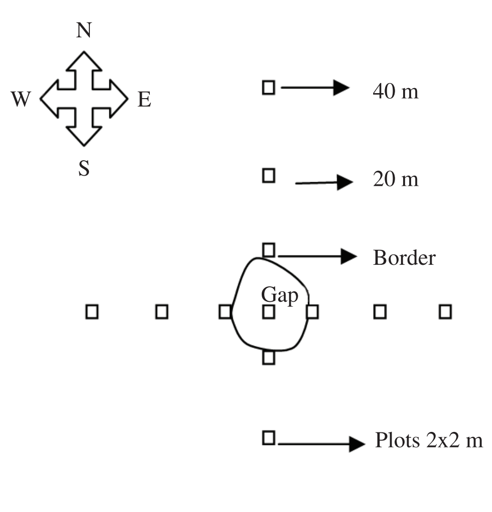

Figure 1. Spatial distribution of natural regeneration samples in relation to the gap.

RR = natural regeneration rate in percentage; A_0 = initial absolute abundance; $A_1 = A_0 + n_i - n_s$ = final absolute abundance; n_i = nº of individuals recruited for the study; n_s = nº of individuals that left the study after mortality.

Recruitment (R%) and mortality (M%) were also assessed through the following equations: $R = (ni/A_0).100$; $M = (n_s/A_0).100$.

Results were statistically analyzed using the BioEstat 5.0 software by parametric analysis of variance (score data) of three factors (center and directions, forest gap size class and study period) according to variables Natural Regeneration Rate, Recruitment and Mortality at 5% probability in order to test the influences of factors in the dependent variables. To this end, data were transformed by the expression Log(xi*xi) and the following hypotheses were elaborated at $\alpha = 0.05$ level:

-H_0: directions (North, South, East and West), gap sizes and study period do not affect Recruitment, Mortality and Natural Regeneration Rate of *C. guianensis*;

-H_1: at least two means of Recruitment, Mortality and Natural Regeneration Rate of *C. guianensis* are significantly different from one another.

3 Results and Discussion

Regarding the Natural Regeneration Rate (RR%), there is sufficient statistical evidence to accept the null hypothesis at $\alpha = 0.05$; with p = 0.5865; considered insignificant, i.e., direction does not affect RR. Positive RR was found for measurements in the first years after logging especially in the West direction (RR=60%) (Figure 2). Under such condition, the value found in the West direction is due to higher solar radiation incidence in the morning, as it is impaired by clouds and rain in the afternoon (ORIANS, 1980), or even because of any other biotic or abiotic factor, which would explain the values in gap center and in the East direction, where RR was null. On the other hand, the presence of matrices to the West

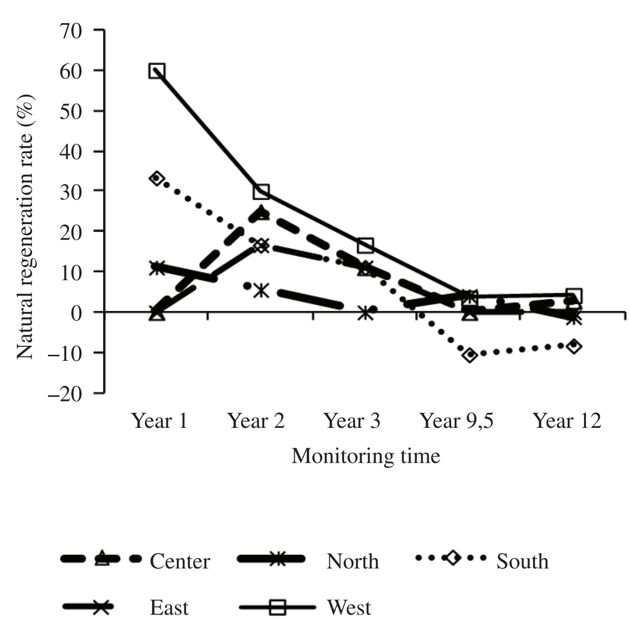

Figure 2. Natural Regeneration Rate of *C. guianensis* in managed forest with respect to direction and time interval.

of gaps may also explain the positive RR in that direction, reaching the plots of the North and South directions.

Natural regeneration occurred in gap center and in the east direction after measurement onset. However, the highest RR found was still in the west direction (30%). Regeneration presence in gap center indicates that incident solar radiation stimulated germination and growth of the species in this area, favoring regeneration dynamics. Micro-environmental differences between gaps must also be considered because of varying gap sizes.

Decreased RR was observed in gap center and in the four directions (Figure 2) throughout the measurements, reflecting the mortality of plants recruited in previous measurements. This may have been caused by canopy cover, which resulted in lower light incidence in the forest ground, thus hindering the recruitment of the species.

In Flona Tapajos, population growth of 13.6%.year^{-1}.ha^{-1} and mortality of 2.2% year^{-1}.ha^{-1} were verified within two years after logging. However, in the subsequent period, recruitment was 41% smaller compared to the previous period, which was attributed to canopy cover, impairing light and hence affecting tree growth (COSTA, 2000); just as in this study with respect to *Couratari guianensis*.

In the latest measurements, RR continued to decline in the center and in the West, East and South directions. In the center and in the East direction, RR=0% was found, that is, recruitment occurred in the early years was compensated by mortality. Therefore, regeneration rate presented value equal to the one found at the onset of measurements. In the South direction, RR was negative as a consequence of the species high mortality in that area. Nevertheless, the North direction was the only one to present increased regeneration rate of *Couratari guianensis*. At the last measurement, corresponding to Year 12 (1998-2010), there was recruitment in the species population in the center and in the West direction. Again, RR=0% was verified in the East - indicating recruitment in this direction. Negative RR was found in the South and North directions, once again due to canopy cover. In this area, the East-West transect generally offers greater amount and quality of photosynthetic active radiation (PAR) to plants (MALHEIROS, 2001), which can explain the behavior of the species. Light intensity and daily insolation are greater in gaps and incident light presents spectral quality different from that under closed canopy cover (DENSLOW; HARTSHORN, 1994). Greater amount of PAR is found in gaps, this is of vital importance to plant development and it is referred as the main variable, which controls the other microclimatic variables (BROWN, 1993).

Throughout the study period, *Couratari guianensis* showed positive regeneration rate in almost all gap size categories (Figure 3). In small gaps, the species presented RR=0% at the beginning of the study, remaining constant until the third year, showing static balance, that is, there was no mortality or recruitment of plantlets. Medium gaps showed RR=50% in the first study year, then this rate began to decrease ending the last study year at RR=0%. This result indicates that, at the beginning of measurements in medium gaps where there was still opening in canopy, the light environment was still benefiting the species with high levels of radiation on the forest ground, favorable to the recruitment of new individuals.

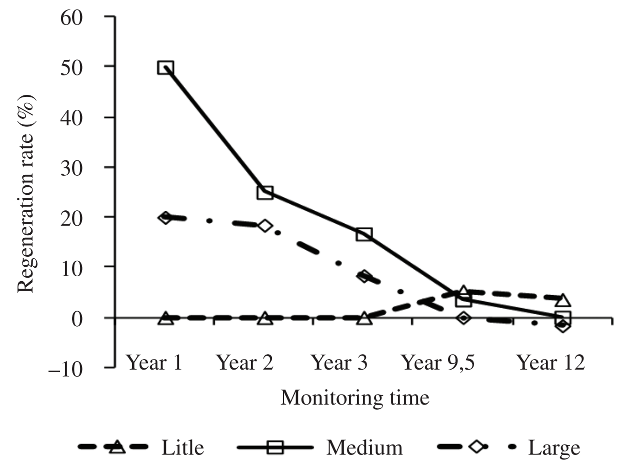

Figure 3. Natural regeneration rate of *C. guianensis* in managed forest with respect to gap size and time interval.

However, during the measurements there was a decrease in RR until the end of the study, indicating high mortality of the species in this area.

Large gaps enable greater incidence of solar radiation. However, in the early years of the study, these gaps presented recruitment rates of *Couratari guianensis* lower than those of medium gaps. This result indicates the existence of another factor limiting the regeneration and development of the species, as the covering of the area by Pioneer vegetation or even grasses, given that their occurrence is propitiated in very open and sunny sites. Vegetation structure dynamics in this area showed an increase of 15% in plant density during the first three years of monitoring (JARDIM; SENA; MIRANDA, 2008). According to Gonçalves et al. (2010), high irradiance, when combined with other stressors, can cause reduced growth or even lead to plant death. Increased RR in small and medium gaps was observed in the measurement of Year 9.5, indicating that recruitment of the species had been occurring in these areas. Thus, the species has ratified its classification in the ecological group of intermediate plants (JARDIM et al., 1996), in which to regenerate and grow species depend on light at varying degrees that are available in both small and medium gaps. Air and soil temperatures are generally higher in gaps and vary widely throughout the day (HUBBELL; FOSTER, 1986). This variation is most pronounced near soil surface (DENSLOW, 1980). Both variables depend on total incident radiation and, therefore, vary according to gap area.

The last year of measurement showed decreased RR of *C. guianensis* for all gap sizes and large gaps reached the end of the study with negative natural regeneration rate for the species.

C. guianensis has presented decreased RR over the monitoring years (Figure 4). This result indicates that recruiting was greater than mortality in the first years of the study, immediately after logging, when gaps propitiated solar radiation of greater intensity. This provided more efficient regeneration during this period resulting in higher RR compared to the previous years.

In the first year of the study, zero recruitment (R=0%) was observed in the center and in the East direction, but it was more significant in the other directions (Figure 5), which may be explained by canopy opening immediately after logging where the environment presented radiation and temperature levels appropriate for seed germination of the species. Seeds from more light demanding genera such as *Cecropia* may remain latent until some unexpected event, such as a gap, expose them to sufficient light to allow germination; while germination of more tolerant species, as *C. guianensis* in this case, may be inhibited coincidently by the occurrence of light (WADSWORTH, 2000).

The following year, 100% recruitment was observed in the center of gaps and 50% recruitment was noted in the East direction, but it decreased in the other directions. At the end of the third study year, only the North direction presented increased recruitment, which lasted until the Year 9.5. The other directions showed decreased recruitment rates reaching zero (R=0%) by the Year 9.5 in the center and by the Year 12 in the East and North directions (Figure 5). This result can be explained by the stage of succession of gaps, where gap opening and closing control the population dynamics of the species through higher or lower radiation levels.

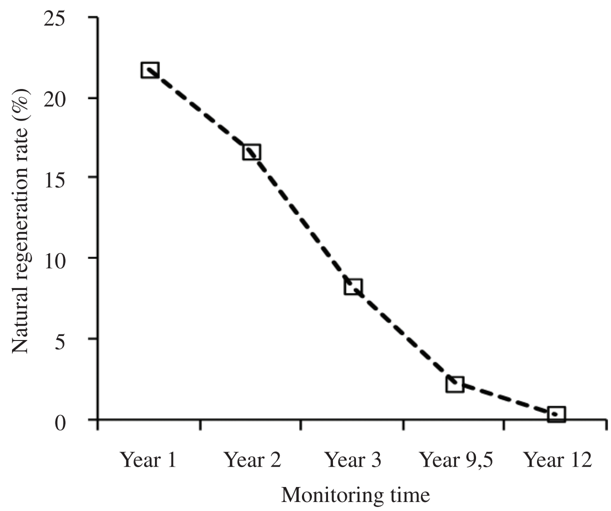

Figure 4. Natural regeneration rate of *C. guianensis* in managed forest regarding time interval.

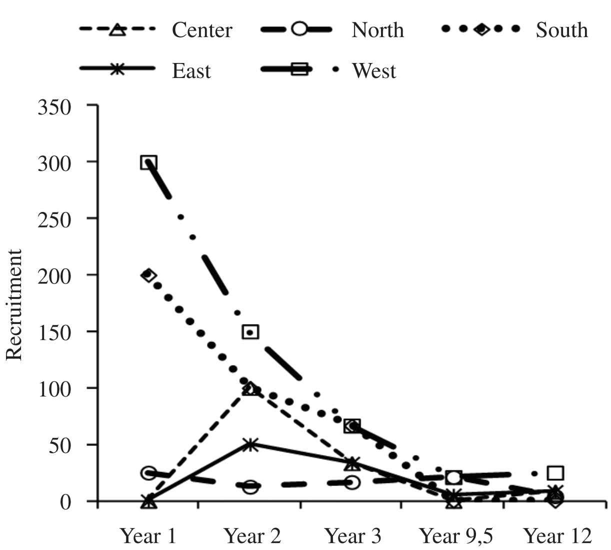

Figure 5. Recruitment of *C. guianensis* in managed forest in Moju, state of Para with respect to gap center and the four directions during the study period.

In the first year of monitoring, medium and large gaps presented high recruitment (Figure 6). In the second year of the study, recruitment increased to 100% compared to the beginning of the research in medium gaps and remained constant in large gaps, but it was null in small gaps until the third year. As of the third year, decreased recruitment was observed in large gaps until reaching zero at the end of the study. This reduction was also verified in medium gaps but only as of the third year of the study.

Once again this result is explained by stage of succession indicating that gradual canopy cover in medium and large gaps was adverse to the recruitment of the species. This species behavior in small gaps corroborates this result despite recruitment occurrence 9.5 years after logging, which was also reduced as in all gap sizes till the end of the study (Figure 6). Concerning recruitment, there is sufficient statistical evidence to reject the null hypothesis at α = 0.05 - given p = 0,0028, which is considered highly significant, that is, time interval does affect recruitment. Santos (2010) found similar values when analyzing *Vouacapoua americana* Aubl. in the same area of study, presenting significant differences especially regarding the third year of research, whose recruitment reached 36,07%.

There was significant reduction in the recruitment of *C. guianensis* over the years (Figure 7) indicating that, during the study period, the environment was not very conducive to the emergence and development of the species, causing the thinning of its population. This result may also be a consequence of stage of succession, as brightness is low with canopy cover making the environment unsuitable for the development of the species

Concerning mortality, there is sufficient statistical evidence to reject the null hypothesis at α = 0.05 - given p = 0.3861, which is considered significant, that is, at least two means are

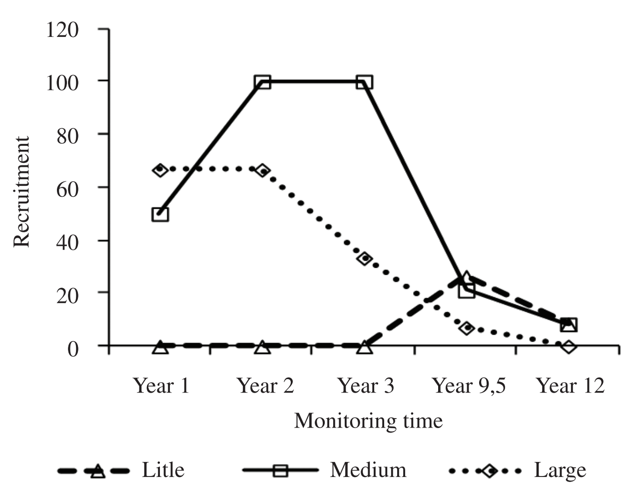

Figure 6. Recruitment of *C. guianensis* in managed forest with respect to gap size by monitoring period.

different. The species presented greater mortality in the South direction (Figure 8) with no significant differences in mortality rate values compared to the other directions.

Measurements began recording mortality of *Couratari guianensis* only in the South direction. No record was performed in the center and in the other directions and the same occurred in the following year (Year 2), but with decreased mortality rate in the South direction (Figure 8). In Year 3, the center and the East and West directions continued not show mortality, while the North direction presented 16.67% mortality rate and the South direction continued to show reduced mortality. In Year 9.5, mortality was not found only in the center, while the North and South directions showed reduced rates and the East and West directions presented mortality for the first time in the study.

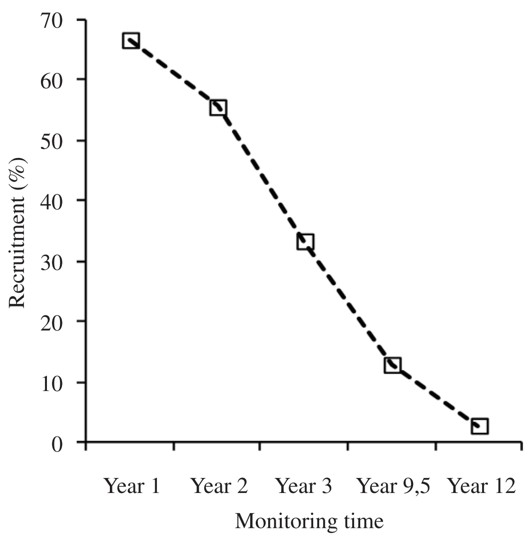

Figure 7. Recruitment of *Couratari guianensis* in managed forest regarding time interval.

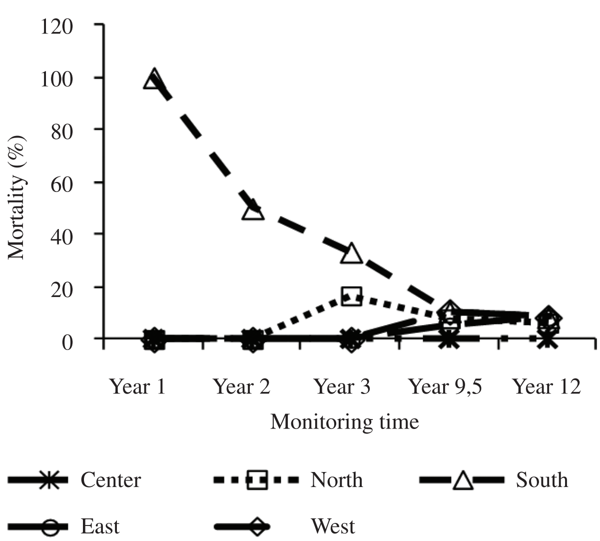

Figure 8. Mortality of *Couratari guianensis* in managed forest with respect to the center of gap and the four directions during the study period.

At the end of monitoring, *Couratari guianensis* showed reduced mortality in the North, South and West directions. The East direction presented a slight increase in mortality rate, characterizing the thinning of the species population, which may have occurred because of the strong interspecific competition in gaps at more advanced stages of succession. Gap center reached the end of the study with no record of mortality.

In the first two years of monitoring, *Couratari guianensis* showed mortality only in large gaps, with reduction in the second year (Figure 9). In Year 3, again there was no record of mortality in small gaps. However, mortality of 33,33% was verified in medium gaps while increased rates were found in large gaps

In Year 9.5 and Year 12, *Couratari guianensis* presented mortality in all forest gap size classes. However, decreased mortality rates were found in medium and large gaps while increased rates were noted in small gaps. Canopy cover may have induced this result, as lower light intensity occurred in medium and large gaps.

The population of *Couratari guianensis* analyzed presented great variation in mortality over time. In the first year, 11.11% mortality was verified and this figure was reduced by half in the second year. In Year 3, an increase in mortality was recorded and a new reduction was found in the fourth year, reaching the rate of 6.48% at the end of the study. (Figure 10). In a study on forest gap enhancement, mortality rate varied from 0 to 53% for intolerant species and from 10 to 18% for three tolerant species (GOMES et al., 2010). Natural regeneration seedlings of *Jacaranda copaia* transplanted to the edge of gaps that were created because of selective timber logging presented average mortality rate of 20% three months after transplantation (NEMER; JARDIM; SERRÃO, 2002), with rate increase observed from the center of gaps into the forest six months after transportation (SERRÃO; JARDIM; NEMER, 2003).

C. guianensis population behavior does not differ from those of most forest species regarding plantlet regeneration (NEMER; JARDIM; SERRÃO, 2002; SERRÃO; JARDIM; NEMER, 2003; BLOOR; GRUBB, 2003). The balance between mortality and recruitment expressed by RR was not influenced either by the North/South and East/West transects

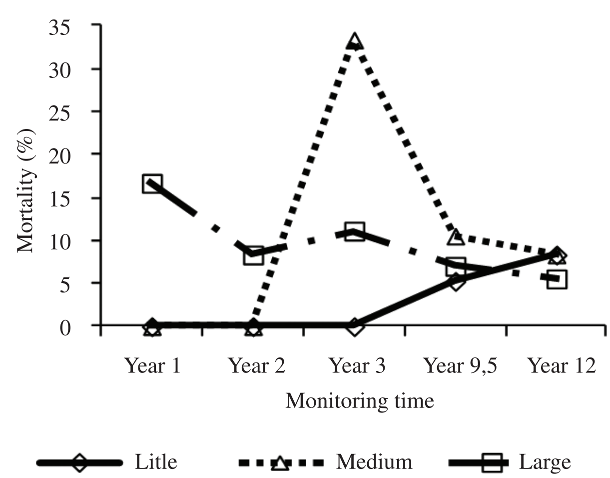

Figure 9. Mortality of *Couratari guianensis* in managed forest according to gap size during the study period.

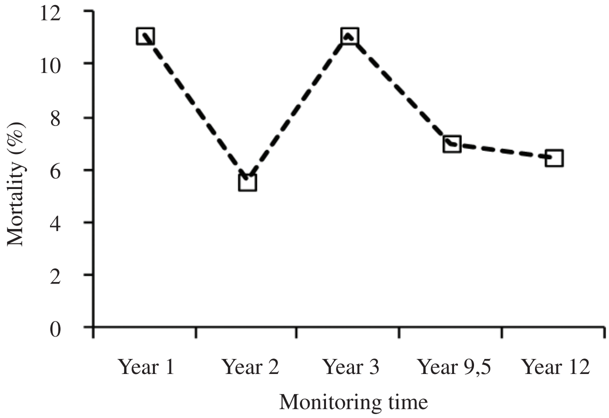

Figure 10. Mortality of *Couratari guianensis* in managed forest according to time interval.

or by gap size due to the strong influence of this factor mainly on recruitment value.

Twelve years after logging, because of canopy cover, radiation inside the forest might have already returned to pre-logging levels, which are quite low (LONGMAN; JENIK, 1981). The mortality of all species studied was insignificant under 10% and 0.8% diffused light, but survival was significantly reduced at 0.2% diffused light (BLOOR; GRUBB, 2003).

Other factors may have influenced the behavior of *C. guianensis* in this study, though. Although not the only factor, annual water deficit above 100 mm, which reduced water availability in the soil, must have been one of the most limiting factors to the development of seedlings of five tree species (PAIVA; POGGIANI, 2000).

4 Conclusions

Couratari guianensis showed alternating behavior over time, which led to a small reduction in its population density caused by mortality and partially compensated by recruitment of new individuals. The regeneration rate of this species has not presented significant differences over time. Nevertheless, significant variations were observed in recruitment and mortality in the directions (North, South, East and West), as well as in gap size (small, medium and large) in the initial stage of growth.

Based on this behavior, it is suggested that the species be classified as intermediate in demand for light and application of regeneration thinning is recommended as a form of managing *Couratari guianensis* population.

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