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Forest regeneration in artificial gaps twelve years after canopy opening in Acre State Western Amazon

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ABSTRACT

The main objectives were to study the effect of gap size and canopy openness on the natural regeneration dynamics considering the parameters of sapling growth, recruitment, mortality, density, species composition and above-ground biomass accumulation. The study was carried out in 32 artificial gaps with sizes varying from 100 to 1200 m^2 and canopy openness from 10 to 45%, from the second to the twelfth year after gap creation. The gap size was measured using the vertical projection of the tree crowns on the ground (Brokaw's definition), and the canopy openness measurement by hemispherical photography. In the first five years, mean sapling growth (0.54 cm $year^{-1}$), mortality (3.9% $year^{-1}$) and AGB (26.2 Mg ha^{-1} or 8.7 Mg ha^{-1} $year^{-1}$) were significantly higher in the gaps than in the forest understorey (0.17 cm $year^{-1}$, 1.5% $year^{-1}$ and −0.59 Mg ha^{-1} $year^{-1}$ respectively) and positively correlated with gap size and canopy openness. In the same period, recruitment was also significantly higher in the gaps (5.8% $year^{-1}$) than in the forest understorey (0.4% $year^{-1}$) but decreased with gap size and negatively correlated with canopy openness. In the first five years, the relative density of pioneer species was higher in the gaps but not significantly correlated with gap size or canopy openness. AGB increased linearly since canopy opening, and twelve years after gap creation it was still higher in larger (121.2 Mg ha^{-1} or 10.1 Mg ha^{-1} $year^{-1}$) rather than smaller (62.5 ha^{-1} or 5.2 ha^{-1} $year^{-1}$) gaps. Twelve years after gap creation there were no significant differences in the parameters of sapling growth, recruitment, and mortality which could be attributed to the original gap size and canopy openness.

1. Introduction

Canopy gaps are recognized as important determinants of tropical forest regeneration (Denslow, 1987; Brokaw and Busing, 2000), initiating a forest cycle of plant germination, establishment and growth. The important variables determining the outcome of this process are gap size, gap age, gap microhabitat type and the surrounding forest (Uhl et al., 1988; Chandrashekara and Ramakrishnan, 1994; Sapkota and Oden, 2009). Tree fall gaps are thought to contribute to species diversity in tropical forests by providing opportunities for niche differentiation in modes of regeneration (Grubb, 1977; Welden et al., 1991; Molino and Sabatier, 2001; Sheil and Burslem, 2003). In this way the gap phase is the most important stage of the forest growth cycle for the determination of the natural regeneration of canopy trees (Whitmore, 1989; Brokaw, 1985a, 1989; Arriaga, 2000). Creation of a gap in the canopy acts on patterns already established in the understorey of the closed phase (Brokaw, 1989).

Unlike forest understorey, a combination of primary and secondary species is found in canopy gaps (Chandrashekara and Ramakrishnan, 1994). Gap creation also triggers the growth of saplings of non-pioneer species, which have the capacity to germinate under closed canopy, and which remain suppressed until a gap is created (Bazzaz and Pickett, 1980; Brokaw, 1985a).

A number of environmental changes occur soon after gap formation in a forest, the magnitude of which is determined by the gap size (Arriaga, 1988). Light availability increases and root competition declines because of the death of trees toward the centre of the gap (Hartshorn, 1978; Brokaw, 1985a,b). In gaps the availability of resources such as water and soil nutrients may temporarily increase (Swaine et al., 1997; Denslow et al., 1990), but the competition for nutrients tends to increase from the opening until around the fifth year.

Changes in temperature and exposure of plants to sunlight affect evaporation and transpiration rates. Different amounts of irradiance usually lead to differences in plants' growth (e.g. Brown, 1996; Tuomela et al., 1996), recruitment and mortality rates, and species composition (e.g. d'Oliveira, 2000) in the gaps. Greater irradiance at the ground level results in a reduced relative humidity and an increased amplitude of temperature fluctuation in gaps compared

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to the forest understorey (Brown, 1993). Irradiance is positively correlated with gap size (Barton et al., 1989; Brown, 1993), but different gap sizes can produce similar irradiance (canopy openness) measurements (Whitmore et al., 1993; d'Oliveira, 2000).

Dependence on canopy opening for germination and sapling establishment has been used to define the difference between pioneer and non-pioneer species (Swaine and Withimore, 1988). However, sapling survival is more likely to be the key factor creating differentiation between species (Swaine and Withimore, 1988; Kennedy and Swaine, 1992). For example, pioneer species undergo high mortality in forest shade but respond strongly to increases in irradiance, while non-pioneers have lower mortality in the shade but respond less strongly to increases in irradiance (Brokaw, 1985a; Kobe et al., 1995; Swaine et al., 1997). These differences between pioneer and non-pioneer species affect the relative density of different types of species in forests with different frequencies or intensities of disturbance (Brokaw, 1989; Molino and Sabatier, 2001).

Logging the forest results in the formation of gaps with a range of different sizes (e.g. Asner et al., 2004), according to the size of the felled tree (e.g. Sapkota and Oden, 2009), topography, surrounding forest structure, logging method (e.g. skidding logs by mechanized techniques Pereira et al., 2002, or animal traction, d'Oliveira and Braz, 2006), and logging intensity. Felling gaps (gaps originated by the felling of a tree) have very variable characteristics. Studies of the influence of the gap size on natural regeneration have been conducted in natural (Brokaw, 1989; Obiri and Lawes, 2004) and artificial gaps (d'Oliveira, 2009). Artificial gaps are used to obtain better control of the experiment in terms of gap characteristics (age, size, topography, orientation, etc.), facilitating analysis of the results. This technique has also been used by several authors to study the early regeneration phase in the natural regeneration of tropical forest (Brown and Whitmore, 1992; Kennedy and Swaine, 1992; Tuomela et al., 1996; Thompson et al., 1998; d'Oliveira, 2000, 2009; Dupuy and Chazdon, 2006, 2008).

This study aims to identify relevant differences in the saplings' growth, recruitment, mortality, species richness and aboveground biomass accumulation, produced by the opening of artificial gaps of different sizes in a forest in Acre State Western Amazon. The main research question is which gap size or gap range can provide the best conditions for the regeneration of canopy species, which have to compete with pioneer species in these gaps, with the goal of sustainable timber production.

2. Methods

2.1. Site description

The experiment was installed in the experimental station of the Embrapa Acre, Latitude 9°58′22″S and Longitude 67°48′40″W, in 1997 (d'Oliveira, 2000) in a tropical moist forest. The predominant soils are dystrophic oxisols, with high clay content. The climate is Awi (Köppen) with annual mean precipitation of 1800 mm; mean daily temperature of 25 °C and a dry season between June and September a period during which rainfall average is usually >100 mm per month (EMBRAPA, 1996a,b).

2.2. Gap creation and plot establishment

The study was carried out in 32 artificial gaps, and the forest understorey was used as a control for the experiments. The artificial gaps were created in 1997 during the dry season from July to August by removing all trees and saplings above 1 m height to create gaps of the required size in the forest of Embrapa Acre Research Station. Brokaw's (1982) gap definition was used for gap size determination (projection of the edge of surrounding tree crowns to the ground). Although this definition has been criticised (e.g. by Popma et al., 1988, who suggest the inclusion of the disturbed area in the edges as a part of the gap, and by Thompson et al., 1998), it was used for its simplicity and because it facilitated the control of gap size (e.g. Nichols et al., 1998). Artificial gaps were created such that gap areas were around 100 m^2 (small), 400 m^2 (medium), 800 m^2 (large) and 1200 m^2 (very large).

The experiment was installed along four compass lines with eight gaps each line. In total there were 16 replicates of the small gaps, eight replicates of the medium gaps, and four replicates of the other sizes.

For the natural regeneration sampling, 5 m wide transects were established along an east-west direction across each gap and for an additional 10 m into the adjacent forest understorey on the one side (Fig. 1). Along the transects, plants were classified according to position starting from the forest understorey to the gap centre in 5 m intervals, assigning ordinal values to each interval according to its distance from forest understorey to gap edge and from gap edge to gap centre. This arrangement was designed to sample the full range of light conditions found along the gradient from closed canopy to the centre of canopy gaps. Four additional 5 m wide and 40 m long transects were established in the forest understorey parallel to the central portion of each of the four gap lines and offset from them by 50 m (Figure 1). The study involved the measurement of saplings growth, recruitment, mortality, density and species richness. All saplings of timber species above 1 m height were tagged, identified and measured (diameter at 0.30 m height). Immediately after gap opening no saplings with more than 1 m height survived. The measurements in the plots started one year after gap opening and were repeated at two (d'Oliveira, 2000, 2009), five and twelve years.

In 2005 the experiment was partially destroyed by incidental fire from neighbouring pastures, affecting the control lines and nine gaps which were removed from the twelfth year analyses.

2.3. Hemispherical photography

Brokaw's (1982) gap definition has been criticised (e.g. Popma et al., 1988) because gaps are defined by their minimum size and the area influenced by them may be greater. In addition, the surrounding forest structure and gap orientation (Brown and Whitmore, 1992) can produce differences on the proportions of photosynthetically active wavelengths (e.g. Denslow et al., 1990). In this work, through the use of hemispherical photography, we studied the effects of the percentage of canopy openness in the gaps regeneration. Immediately after gap creation, hemispherical photographs were taken to measure the percentage of canopy openness (Whitmore et al., 1993; Ferment et al., 2001). The photographs were taken at the gap centre, 1.3 m above-ground on cloudy days at the end of the dry season (October 1997). To obtain the canopy openness percentage the hemisphere photographs were digitized and processed by Winphot version 4.0 (Ter Steege, 1994).

2.4. Data manipulation and analysis

2.4.1. Growth rates

Growth rates from the second to the fifth year after gap creation were calculated by the formula:

$$\frac{dbh_2 - dbh_1}{time}$$

where

dbh_1 – diameter of the tree in a previous census;