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Full Research Article

Growth of Forest Stands and Tree Species Ecological Guilds in Undisturbed and Selectively Logged Amazonian Forests, Northern Brazil

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Abstract

The growth of trees in forest canopy gaps left by the felling of adult commercial trees has been shown to differ for individual ecological guilds of tree species and initial site conditions prior to logging. The objective of this study was to identify patterns in individual tree diameter growth both for the tree population overall and as a function of ecological guild in specific for undisturbed and selectively logged forest and compare between the two. Data came from two areas of non-flooded forest of the Brazilian Amazon in the states of Amazonas and Para for trees with dbh ≥10 cm. For purposes of statistical analysis tree species were clustered in three ecological guilds based on bole wood specific gravity and successional status. Tree growth irrespective of ecological species guild in the vicinity of logging gaps for the three year period following the harvest event was significantly more elevated in relation to undisturbed forest and this positive difference was proportionately greater for Amazonas in relation to Para. Ecological guilds showed a pattern of increasing growth rate with decreasing bole wood specific gravity and successional status when area and site disturbance status where not taken under account. In response to logging all ecological guilds showed increased growth rates but all were proportional to levels found in the undisturbed forest. Tree species life history characteristics appear to be a more significant factor affecting tree growth than site disturbance status in response to logging at least for the first 3 years after the logging event.

1. Introduction

Selective timber harvesting is currently one of the main forms of anthropogenic disturbance for forests of the Brazilian Amazon (Laurance et al., 2004). The effect on the forest ecosystem of this is therefore of great scientific importance. Harvesting in these areas is highly selective typically removing only a few top quality trees ≥50 cm dbh. It has been hypothesized that under these conditions forest stand growth is increased primarily due to the growth of more fast growing early successional tree species that are favored in relation to more slow growing late successional ones because of the shift to increased disturbance and altered stress conditions that are more suitable for their growth but also survival and recruitment (Silva, 1989; Silva et al., 1995; Finnegan, 1999; Arets, 2005; Herault et al., 2010). A further reason advocated is the decrease in competition as a result of the reduction in stand density promoting the growth of all remaining un-harvested stems in the residual stand (Higuchi and Favrichon, 1995; Silva et al., 1995; D' Oliveira, 2000; Carvel et al., 2004). This research was conducted in order to evaluate the impact of selective logging on stand and individual ecological guild growth and to compare differences with undisturbed forest both within and between them for two non-flooded tropical forest areas of the Brazilian Amazon over an average period of three calendar years. Our hypothesis was that in response to logging disturbance increased stand level growth rates in relation to undisturbed forest occurs due to the increased performance of more heliophilic earlier successional tree species groups in relation to more late successional shade tolerant ones.

2. Materials and Methods

2.1. Study sites

The four study sites in the two areas in the states of Amazonas and Para (Figure 1) where: (1) The Precious wood Amazonas ltd site outside Itacoaitiara operated by the aforementioned private wood production company, located about 120 km south of the city of Manaus, Brazil (3°0’28.57”S, 58°39’48.76”W); (2) The Adolpho Duke forest reserve located about 50 km south of the city of Manaus, Brazil (2°57’14”S,59°55’49”W); (3) The Tapajos km 83 site in the Tapajos national forest, located about 75 km south of the city of Santarem, Brazil (2°58’24.02”S, 54°56’46.45”W); (4) The Tapajos km 67 site also in the Tapajos national forest, located about 56 km south of the city of Santarem, Brazil (2°51’25.20”S, 54°57’32.40”W). Mean annual rainfall in Manaus measured between 1961 and 1990 was 2,285 mm, more than the average annual rainfall of 1,909 mm in Santarem for the period from 1967 to 1990 (INMET, 2001; NuRMA, 2002). The major climatic difference among the sites is the seasonality of the distribution of rainfall resulting in a distinct dry season with a different length in Amazonas in relation to Para. We define the dry season length here as the number of months with rainfall averaging <100 mm month^{-1} (Sombroek, 2001). Amazonas experiences the shortest dry season (3 months, July-September) and Para the longest (5 months, July-November). Soils in Amazonas and Para are clay-rich Oxisols with low organic C content, low pH, low effective cation exchange capacity, and high aluminum saturation (Chauvel et al., 1987; Parotta et al., 1995; Telles et al., 2003). Overall relief varies among the two areas, though sites where in upland (terra- firme) forest, with slopes <10%. The two areas are classed as tropical moist forest in the Holdrige life zone classification (Holdridge, 1978) and are both classed as terra fime (non-flooded).The forest of the Amazonas area is exceptionally rich in tree species (more than 280 tree species considering trees >10 cm dbh) with a consequently very low dominance on a per hectare basis(in relation to the Madre de dios site with only 180 tree species per hectare on average considering trees >10 cm dbh (ter Steege et al., 2003). There are also considerable variations in terms of biomass and its dynamics (Malhi et al., 2004) as well as stand structure for forests of these sites (ter Steege et al., 2003). More specifically forests of Para state area have much lower stem density in relation to Amazonas (450 stems >10 cm dbh in Para viz. 500 stems in Amazonas). Also the forests of Amazonas exhibit a decreased dynamism of biomass turnover in relation to Para (1.8 Mg C ha^{-1} a^{-1} on average in Amazonas viz. 4 Mg C ha^{-1} a^{-1} in Para).Finally the forests of Para contain more earlier successional low wood density light loving tree species in relation to Amazonas (ter Steege et al., 2006)

2.2. Selective logging operations

Logging and silvicultural treatment took place only at the PWA ltd and Tapajos km 83 sites. In both these sites where timber was harvested logging was highly selective removing only 2 to 4 commercial trees per hectare on average of the legal minimum felling diameter (MFD) of 50 cm dbh . In each of the two sites reduced impact logging techniques where applied in order that the timber be extracted. The general philosophy behind this is to minimize environmental impact of logging and extraction operations on the area of forest. They are considered naturally to be more environmentally benign than so called conventional logging techniques. A detailed description of such operations can be found in Sist et al. (2003) and FAO (2004). In the PWA ltd site light post exploitation silvicultural treatment aimed at releasing potential crop trees (PCT’s) was additionally applied by girdling noncommercial trees competing with selected commercial ones, with the aim of increasing future total economic yield from the forest.

2.3. Monitoring protocols

Diameter growth data on trees where available from both

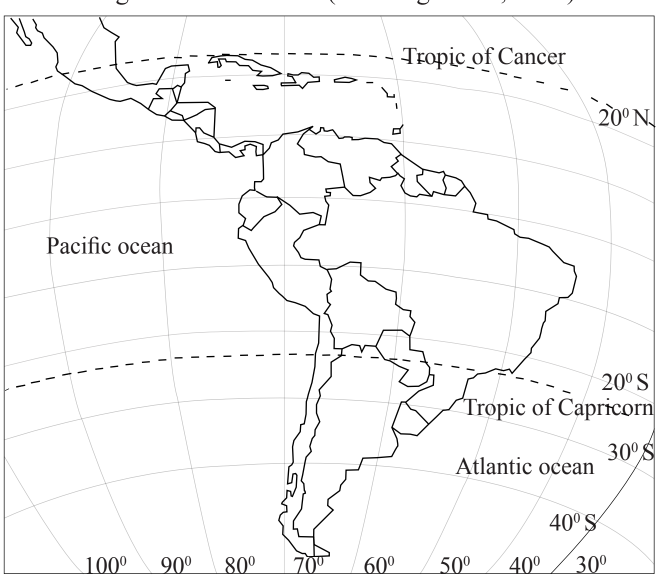

Figure 1: Geographical location of the four study sites in the two areas in the states of Amazonas 1: PWA Ltd; 2: Adolpho duke; 3: Tapajos KM 83; 4: Tapajos KM 67.

Amazonas and Para states across the four sites (PWA ltd, Adolpho Duke, Km 83 Tapajos, Km 67 Tapajos) from sample plots designed to monitor changes in the dynamics of the tree community. At all sites except the PWA ltd site all trees ≥10 cm diameter at breast height (dbh) mapped within each permanent plot were identified to the genus/species level. At the PWA site the minimum dbh for a tree was 15 cm. In all sites we took advantage of plots established prior to this study. As a result the area and layout of permanent plots differs among the three sites. They are described extensively bellow.

The Adolpho Duke plots are located in the Adolpho Duke Forest reserve are the first. They comprise 72 plots each of 0.96 ha .Plots do not have a fixed shape but are transects that follow what relevant topographic gradient is present. They are curvilinear in shape as a function of that. Within these sub samples based on size are taken for trees down to 1 cm dbh. For the purposes of this study minimum size made available was 10 cm .They have been measured in 2004 and another in 2008. Castilho et al. (2006) provide details of the data and the environment of the plots.

The PWA ltd plots are the second. They located in the private forest lands of Precious woods limited Amazonas. Plots are rectangular in shape and are of 0.5 ha (50×100m) in size and are artificially subdivided in 10×10 m^2 subplots. They are comprised of 18 plots in total. Within each plot trees of a minimum size of 15 cm dbh are selected for measurement according to specific criteria as follows- all trees of all species down to 50 cm dbh, trees below that and down to 30 cm dbh only if they are classed as commercial or potentially commercial. The same for trees between 30 to 15 cm dbh but only on 50% of the subplots selected to be in and around parts of the plot affected by selective logging and timber extraction. They have been measured two times one in 2003 and another in 2006 after logging and silvicultural treatment. . Wellhöfer (2002) provides details of the environment of these plots.

The KM 83 plots are located in the Tapajos national forest. They comprise a series of transect plots in which trees ≥10 cm dbh have been monitored at monthly intervals since 2003 and up to 2009. Measurements began exactly one year prior to any logging operation so that related differences may be studied. A semi random sample has been taken by which trees in areas of the forest definitely in the vicinity of logging gaps are selected. Figueira et al. (2008) provide details on the data and environment of these plots.

The Km 67 plots are also located in the Tapajos national forest. They are essentially a linear 9 hatransect in which trees are measured on a censored inventory basis with a minimum dbh of 10 cm (subsample for trees ≥10 cm and all ≥35 cm). They have been censuced three times in 1999, 2001 and 2005. For the purposes of this study the latter two where only used. Quesada et al. (2006) provide details on the data and environment of these plots.

The criterion for selecting trees to be considered for our analysis was that of being inside logging gaps. This meant to be inside the area of damage of the falling tree as defined by Phillips et al. (2004). Essentially The area of damage was measured and was proportional to crown surface area of the felled tree (Figure 2)

2.4. Tree species ecological grouping

All trees of all species ≥10 cm dbh found in all plots that were monitored over the time period where classified a priori using all possible combinations of three bole wood specific density (g cm^{-3}) and three maximum potential height classes. These are traits which are known to correlate well with the individual processes of growth, recruitment and mortality as well as with

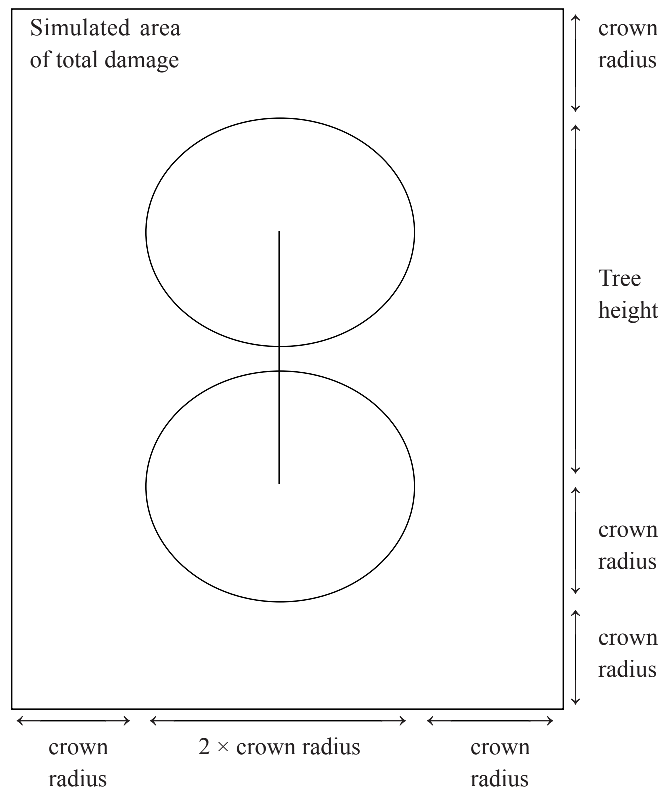

Figure 2: The Phillips et al. (2004) procedure for selecting trees in areas affected by selective logging, Trees were considered to be inside a logging gap if they were inside the area of damage created by the fall of a large tree or group of trees. For an individual fallen tree of the legal harvestable diameter of 50 cm dbh this was a rectangle with dimensions four times crown radius by three times crown radius plus tree height. The heavy lines represent the stem and crown of the tree in their positions after tree-fall, with the lighter circle representing the original position of the crown before tree fall.

the process of ecological succession (Swaine and Whitmore, 1988; King et al., 2005; King et al., 2006; Kholer et al., 2000; Gourlet-Fleury et al., 2005; Poorter et al., 2008).They are therefore ideal for the purposes of this study. This resulted in three ecological guilds. The respective ecological characteristics of these guilds along with example species varied according to the trait combination of each guild (Table 1).

2.5 Data treatment and statistical analysis

Permanent sample plot data for all trees ≥10 cm dbh was made available for a period of at least three calendar years for all permanent sample plot sites. For the purposes of this study data from only two monitoring campaign where used when more was available. The ones closest in time where selected from each for analysis. The variable used to describe growth of trees ≥10 cm dbh was annual diameter growth rate in centimeter per year using the equation (Equation 1) proposed by Clark and Clark (1992).

$$\frac{dbh2\text{-}dbh1}{t} \qquad (1)$$

Where dbh1 is the diameter at breast height of a tree at the beginning of an inter-census period, dbh2 is the diameter at breast height at the end and t is the time in calendar years between measurements.

The objective of the analysis was to test for differences between the ecological guilds with respect to disturbance status of the site (undisturbed forest vs. logging gap) both within and between the two areas. For the purposes of the analysis we defined four sites by dividing each of the two areas in their respective primary and logging gaps habitats for each of which there where three ecological guilds. Diameter growth data was analyzed by an analysis of variance using the general linear modeling (GLM) subroutine of the statistical package GENSTAT v 12.1.

3. Results and Discussion

Tree diameter growth of all stems ≥10 cm dbh irrespective of ecological guild was significantly different between the two areas for the undisturbed forest (p<0.001), (Figure 3). In the period after the logging event tree growth was significantly different between the two areas for the selective logging gap habitat both between them and in relation to the undisturbed forest within each individual area (p<0.001) This was also the case when comparing with the undisturbed forest site of the other area (p<0.001).The decreased competition in logging gaps apparently favored all remaining stems due to additional space, light and other resources essential for growth becoming available. This is in agreement with several studies both in Amazonia (Silva, 1989; Silva et al., 1995; Arets, 2005; Figueira et al., 2008; Herault et al., 2010) and elsewhere (Kamessheidt et al., 2003) .Conditions inside logging gaps in these forest can potentially be more favorable to growth (van Dam, 2001) as there is a generally competition free environment and increased light availability in relation to undisturbed forest at least for the average gap size of this study. The greater positive difference in magnitude of the Amazonas area in relation to Para can be explained potentially by the additional silvicultural treatment in that site of potential crop tree release of commercial trees in non-merchantable sizes.

As far as diameter growth of all stems ≥10 cm dbh irrespective of area or site disturbance status, there was a statistically significant difference between the three ecological guilds (p<0.001). The guilds showed a pattern of increased diameter growth rate with decreasing wood specific gravity, maximum potential height class and therefore successional status (Figure 4). More specifically the true pioneers showed greater mean diameter growth rate in relation to light hardwoods and even more so with climax. This is in agreement with previous studies in primary unlogged (D'Oliveira, 2000; Arets, 2005; King et al., 2005; King et al., 2006; Poorter et al., 2008; Herault et al.,

Table 1: Trait statistics of ecological species guilds used and example tree species

Guild	Bole wood density (g m^{-3})	Maximum potential height (m)	Example species
Climax	≥0.49	≥5	*Hymenea courbraril*
LHW	<0.49	>10	*Goupia glabra*
Pioneers	<0.49	<15	*Cecropia sciadophylla*

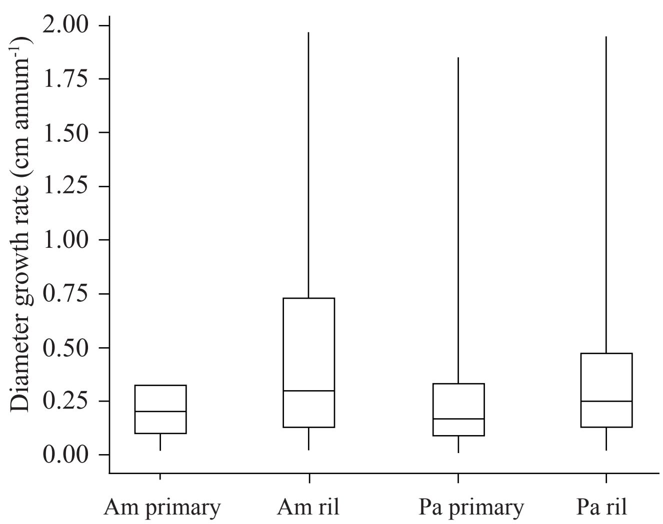

Figure 3: Box-and-whisker diagram of the mean annual diameter growth in cm annum^{-1} by site (Amazonas=Am, Para=PA) and disturbance status (selectively logged under reduced impact logging guidelines=RIL, undisturbed=primary)

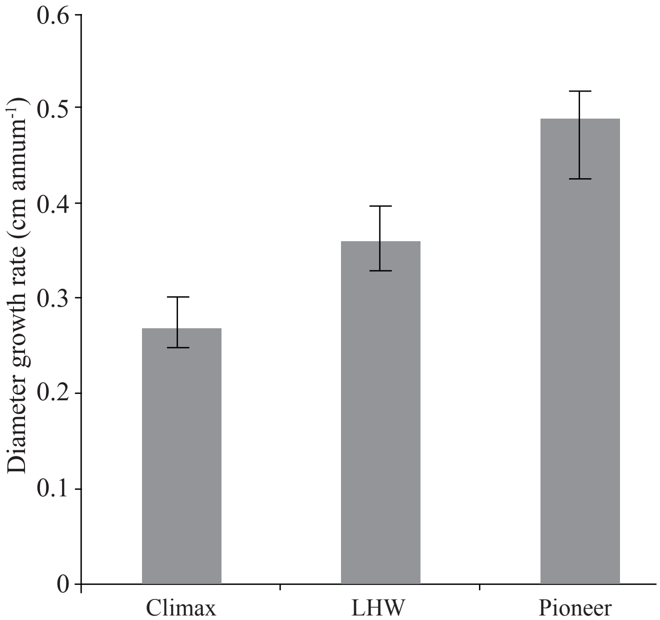

Figure 4: Mean diameter growth rate in cm per annum by ecological guild irrespective of area or site disturbance status. Error bars represent the standard error of the mean.

2011; Karfakis and Andrade, 2013), drought affected (Karfakis and Andrade, 2013) or previously undisturbed selectively logged forest (Silva, 1989; Finnegan et al., 1999; da Silva, 2004; Herault et al., 2010).Tree species or individual trees that will grow faster will tend to have a lighter bole specific wood gravity as a consequence of wider spaced tree stem rings for a given size of tree in relation to those with narrower and hence greater wood density when differences in site conditions are not taken into account (Jeffries, 2008). Furthermore, data sets for species of later succesional guilds will generally contain trees of larger sizes which will tend to grow slower due to both size and age (Bowman et al., 2013). For PWA, tree diameter growth of all stems ≥10 cm dbh irrespective of ecological guild was significantly different between the two areas for the undisturbed forest (p<0.001) (Figure 5). In the period after the logging event tree growth was significantly different between the two areas for the selective logging gap sites both between them and in relation to the undisturbed forest within each individual area (p<0.001) This was also the case when comparing with the undisturbed forest site of the other area (p<0.001). The decreased competition in logging gaps apparently favored all remaining stems due to additional space, light and other resources essential for growth becoming available. This is in agreement with several studies both in Amazonia (Silva, 1989; Silva et al., 1995; Arets, 2005; Herault et al., 2010) and elsewhere (Kamessheidt et al., 2003) .Conditions inside logging gaps in these forest can potentially be more favorable to growth (van Dam, 2001) as there is a generally competition free environment and increased light

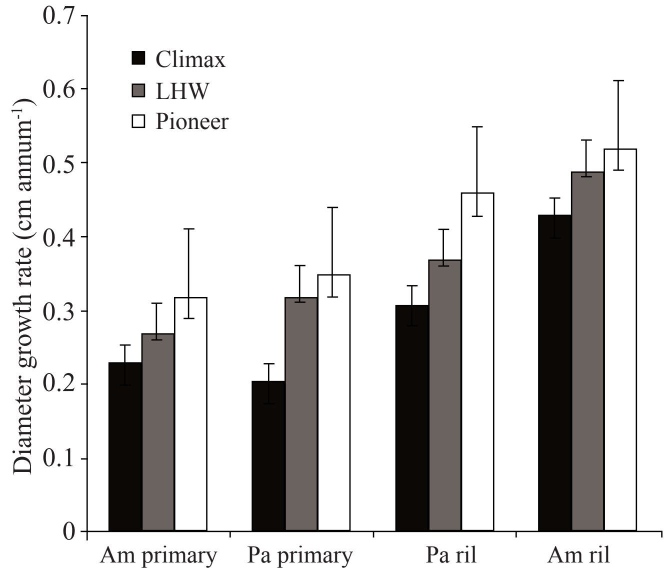

Figure 5: Mean annual diameter growth rate in cm/year by ecological group (Climax, LHW-light hardwoods, pioneers=true pioneers) for the Para (PA) and the Amazonas (AM) area by site and respective disturbance category (RIL-reduced impact logging, Primary-unlogged). Error bars represent the standard error of the mean.

availability in relation to undisturbed forest at least for the average gap size of this study. The greater positive difference in magnitude of the Amazonas area in relation to Para can be explained potentially by the additional silvicultural treatment in that site of potential crop tree release of commercial trees in non-merchantable sizes.

4. Conclusions

Volume increment of residual trees in gaps was increased and all ecological species guilds responded proportionately to release from competition in relation to the baseline levels found in undisturbed forest. This implies that species inherent life history characteristics are more important than species or guild specific differential response to the disturbance event. These results lead us to reject the null hypothesis that in response to logging disturbance increased stand level growth rates in relation to undisturbed forest occurs due to the increased performance of more heliophilic earlier successional tree species in relation to more late successional shade tolerant ones.

5. Acknowledgments

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