

Dynamics of Functional Composition of a Brazilian Tropical Forest in Response to Drought Stress

Theodore N.S. Karfakis, and Anna Andrade

Abstract—The aim of this study was to examine the dynamics of functional composition of a non flooded Amazonian forest in response to drought stress in terms of diameter growth, recruitment and mortality. The survey was carried out in the continuous forest of the Biological dynamics of forest fragments project 90 km outside the city of Manaus, state of Amazonas Brazil. All stems ≥ 10 cm dbh were identified to species level and monitored in 18 one hectare permanent sample plots from 1981 to 2004. For statistical analysis all species were aggregated in three ecological guilds. Two distinct drought events occurred in 1983 and 1997. Results showed that more early successional species performed better than later successional ones. Response was significant for both events but for the 1997 event this was more pronounced possibly because of the fact that the event was in the middle of the dry rather than the wet period as was the 1983 one.

Keywords—Brazil, functional composition, drought, Amazonian non flooded forest.

I. INTRODUCTION

BRAZILIAN Amazonia contains the largest area of remaining tropical forest in the world and is regarded as a cradle of biological diversity at the global level [17],[23],[24]. Therefore the quantification and study of any form of perturbation on this system is of great scientific importance. The most common form of non anthropogenic disturbance upon Amazonian forests is drought stress related tree death leading to opening of the canopy [5],[15],[17]. Droughts in the Amazon are expected to increase in both intensity and frequency in the near future mostly as a result of climate change [1],[5],[6],[17]. Trees of certain more drought prone species are expected to be at greater relative risk especially those individuals that are canopy and emergent trees [25],[27] and thereby creating problems for the associated biodiversity they contain. This form of disturbance has been proven to be directly measurable on the trees which are the physiognomic dominant of the community by periodic mensuration of permanent sample plots [14],[17]. Several studies have dealt with the impact of drought stress on the structural dynamics of Amazonian non flooded forests. However few studies so far are dealing with the functional composition of these forests and their response to drought stress [6],[21]. This is an important area of study because the

true magnitude of the impact of these changes cannot be inferred using structural variables alone [16],[21]. In studies dealing with functional composition response to disturbance in these forests such as logging or succession of former agricultural land it is common to aggregate tree species into a small number of ecological guilds for purposes of statistical analysis [8],[11],[22]. This is because of the relatively small numbers of individuals per species per unit area in the sample plots used to study these [8]. The aim of this study was to evaluate the impact of two successive drought events on the dynamic turnover of ecological guilds of trees on a non flooded tropical forest site of the Brazilian Amazon over large periods of time.

II. MATERIALS AND METHODS

A. Study Site

The study was carried out in the Biological dynamics of forest fragments reserve in the center of non flooded continuous forest undisturbed by any human activity [12]. The area is situated 90 km outside the city of Manaus, state of Amazonas, Brazil (2°51'31.24"S; 59°53'17.36"W; altitude 50 m above sea level) on soils classed as sandy to clayey loam. The area has a moist tropical climate characterized by a period of high precipitation from December to May and five months of low precipitation from June to November. With minor variations, humidity remains high at 70% to 85% throughout the year. The site experienced two strong El Niño driven drought events one in 1983 and another in 1997 during which 50% of the mean annual precipitation fell.

B. Monitoring Protocol

The monitoring of the forest was conducted by the periodic re-measurement of permanent sample plots. In each square 1ha (100mx100m) plot all trees ≥ 10 cm dbh are measured for their diameter and new individuals recruiting in the minimum dbh are identified at the species level and tagged in each subsequent census with a concurrent note of the trees in all size classes that died. Each plot is subdivided into 25 square subplots for purposes of mensuration. A total of 18 plots were used for this study

C. Tree Species Ecological Grouping

For the purposes of this research the FAO convention of the definition of a tree species was used which was that of a woody perennial of a maximum potential height of at least 5 m. We classified all tree species a priori using all possible combinations of three bole wood specific gravity (g cm^{-3}) and three adult stature classes (maximum potential height

Theodore N.S. Karfakis is with the Division of Ecology and Evolution in the unit of Ecology, Imperial College of Science, Technology and Medicine, Ascot, SL5 7PY UK (e-mail: theokarfak@gmail.com).

Anna Andrade is with the Biological dynamics of forest fragments project, National Institute for Research in the Amazon (INPA) Manaus, Amazonas, Brazil (e-mail: titina@inpa.gov.br).

classes). These are traits which are known to correlate well with the individual processes of growth, recruitment and mortality as well as with the process of ecological succession [9],[10],[11],[18]. The result of this was three groups or guilds. These were climax or late successional tree species that are characteristically shade tolerant and have the relatively longest average lifespan in relation to the other tree species, light hardwoods (LHW) species that are present in climax forest but are relatively more light demanding, live for shorter periods of time and respond more favorably to disturbance. Finally the true pioneers are the group of trees that have the lowest possible wood density, have the shortest life cycle and are characteristically the first tree colonizers of a site that has been completely denuded of trees. The respective ecological characteristics of these groups along with the most abundant individual tree species in the permanent sample plots varied according to the trait combination of each group (Table D).

D. Data Treatment and Statistical Analysis

Permanent sample plot data was made available for the period 1981 to 2004. All plots chosen were measured simultaneously in time. This was done to allow for the effect of the drought to be the same in the space of time across the plots. Three variables were used to describe response of each individual ecological group to drought disturbance. The first was annual diameter growth rate in centimeter per year using the equation proposed by Clark and Clark (1992). Reference [2] gives details of the theoretical and practical justification of using this. Here dbh1 is the diameter at breast height of a tree at the beginning of an intercensal period, dbh2 is the diameter at breast height at the end and t is the time in calendar years between measurements. Equation (1) describes this.

$$(dbh2 - dbh1)/t \quad (1)$$

The second was annualized plot percentage mortality rate while the third was annualized plot percentage recruitment rate for each individual guild using the equation proposed by Sheil *et al.*, (1995) for mortality (m) where N_0 is the total number of stems of the particular functional group at the beginning of the time interval t, and N_m is the number of recorded dead trees during the interval. References [19],[20] give details on the theoretical and practical justification for using this. Equation (2) describes this.

$$m = 1 - \left[\frac{N_0 - N_m}{N_0} \right]^{1/t} \quad (2)$$

And the algebraically equivalent equation proposed by Sheil *et al.*, (1996) for recruitment (r) where N_t is the total number of stems at the end of the time interval t and N_i is the number of recorded recruits (i.e. ingrowths) in the particular size class during interval t. References [19],[20] give details on the theoretical and practical justification of this Equation

(3) describes this.

$$r = 1 - \left[1 - \frac{N_i}{N_t} \right]^{1/t} \quad (3)$$

Prior to analysis the appropriate correction factor proposed by Lewis *et al.*, (2004) was applied to all recruitment and mortality observations to make the assumption that time intervals where equal to one year valid. Where λ is the uncorrected rate λ_{corr} is the corrected rate and t is the time between censuses in years. This factor is based on intensive data analyses from a relatively large forest dynamics plot network across the humid tropics. Reference [13] gives details on the practical justification and methodology used to derive this. Equation (4) describes this.

$$\lambda_{corr} = \lambda * t^{0.08} \quad (4)$$

This methodology ensured that valid aggregations of meaningful quantities were performed while changes in these quantities were not affected by differences in measurement campaign dates. Data were analyzed using the GENSTAT v 12.1 software. Analyses were done using repeated measures analysis of variance (mixed regression) for 4 intercensal periods of which that were artificially equal to one year as the interval between successive measurements of a plot was greater than one year. The objective was a comparison across the three groups with time. The drought periods fell in the intercensal periods 1 to 2 for the 1983 event and 3 to 4 for the 1997 event respectively.

II. RESULTS AND DISCUSSION

As far as diameter growth of all stems ≥ 10 cm dbh was concerned there was a statistically significant difference with time across the different groups ($p < 0.001$). The groups showed essentially the same pattern of decrease in mean annual diameter growth during a drought period and recovery afterwards but the magnitude of that recovery differed between the groups (Fig 1a). Recovery from the first event and response and recovery to the second event was related to ecological group while there did not appear to be any correlation with ecological group for response to the first drought event (Table II). The overall pattern was that of a gradient of response that was a function of ecological status. More specifically the more shade intolerant early successional species seemed to recover better than climax forest species with the true pioneers showing a greater magnitude of response than the light hardwoods with the climax species showing the least. This is in agreement with earlier studies [5],[7],[21],[25] and practical knowledge of response to disturbance [26].

TABLE I
ECOLOGICAL GUILDS OF TREES USED IN THIS STUDY, THEIR RESPECTIVE TRAIT STATISTICS AND EXAMPLE TREE SPECIES

Name	Bole Wood Density (g cm^{-3})	Average Adult Stature (m)	Example Species
Climax	≥ 0.49	≥ 5	<i>Hymenaea courbraril</i>
Light hardwoods(LHW)	< 0.49	> 10	<i>Goupia glabra</i>
Pioneers	< 0.49	< 15	<i>Cecropia sciadophylla</i>

TABLE II
COMPONENT VARIANCE ANALYSIS RESULTS FOR ANNUAL DIAMETER GROWTH, CORRECTED ANNUALIZED MORTALITY, CORRECTED ANNUALIZED RECRUITMENT BETWEEN ECOLOGICAL GUILDS ACROSS THE TIME PERIODS MONITORED

Turnover Component	Variable Type		Time Period			
	Ecological Guild		1	2	3	4
Annual Diameter Growth(cm yr^{-1})	1		0.000	0.002	0.001	0.004
	2		0.000	0.087	0.052	0.087
	3		0.000	0.103	0.053	0.085
Corrected Annualized Mortality(%)	1		0.000	0.000	0.000	0.000
	2		0.000	0.041	0.124	0.199
	3		0.000	0.163	0.619	0.463
Corrected Annualized Recruitment (%)	1		0.000	0.000	0.000	0.000
	2		0.000	0.042	0.103	0.209
	3		0.000	0.102	0.758	0.338

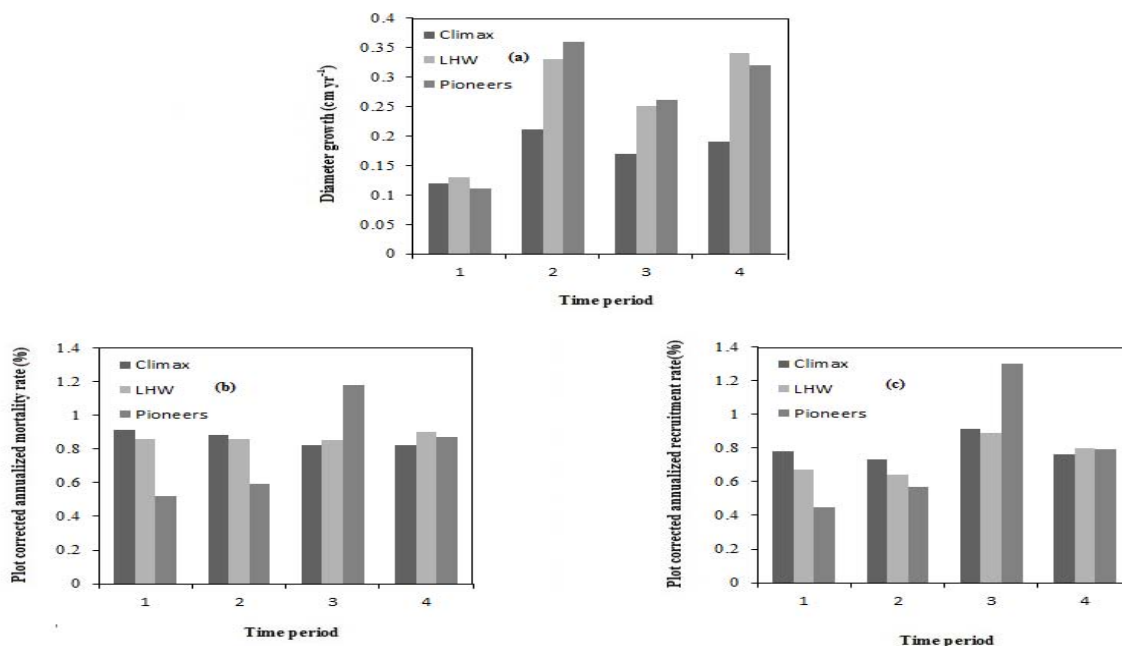


Fig. 1 Patterns in the behavior of the three ecological guilds across the four intercensus periods with time in stem diameter growth in cm yr^{-1} (a), corrected annualized mortality percent (b), and corrected annualized recruitment percent (c)

Tree species that are more adapted to disturbance and earlier successional will also be able to cope with drought more effectively due to their ecophysiological traits and overall ecology which is adapted to conditions that are more limiting to tree growth and survival than the ones of mature forest such as open ground.[15],[16].

Moving on to corrected percentage mortality rates there was a statistically significant difference in mortality rates between

the different groups with time ($p=0.019$). During a drought period there was increased mortality of tree stems for all groups possibly as a result of increased stress for water across the site a common effect of drought disturbance[1],[5],[15]. It would seem that during a drought mortality was more elevated for earlier successional species relative to later successional ones (Table II, Fig. 1b). This was not an expected pattern as such species are considered to be more adapted to drought

stress due to their relatively greater tolerance of more open and hence higher desiccation risk conditions[5]. A gradient of response magnitude was observed with climax species showing less difference in relation to pre and post drought periods. A possible explanation for this pattern may have been the spatial position of trees in the forest as a function of their ecology. Early successional species will tend to grow in sites with increased exposure to light initially because their seeds or sprouts would have required relatively high light conditions in which to germinate and develop respectively[3],[4]. Their position afterwards if site conditions were maintained would be unfavorable during a drought due to increased exposure of these trees to irradiance and hence drought stress. However as suitable data on spatial position were lacking and with other contributing microsite factors such as soil or topography interacting to produce the final effect, this theory remains untested.

Finally as far as corrected percentage recruitment was concerned there was a statistically significant difference between groups with time was observed ($p < 0.001$). An overall increase in mean annual recruitment rate occurred after a drought that was more evident for the 1997 event in relation to the 1983 one (Table II, Fig.1c). These results are in agreement with expected ecological response to such disturbance[8],[21]. The increased disturbance in the forest which creates a much larger amount of microsites relative to the pre disturbance period in terms of soil and increased light conditions that is a direct result of the increased death of canopy trees. Tree species that were more early successional exhibited higher recruitment rates immediately after a drought relative to more late successional ones. The light hardwoods were intermediate and the climax species were last in showing change. This can be explained by the ecological characteristics of tree species in these groups [22],[26].

IV. CONCLUSION

The two drought events had a similar impact on the functional composition dynamics of the forest. However the first drought event of 1983 based on available data had a less significant effect relative to the second of 1997. This probably is related to the type of drought event. Overall the system responded to this form of disturbance significantly and in a way that would be expected from disturbance caused by the mortality rates of mostly canopy and emergent size trees. Based on the above we can conclude that drought disturbance is a major determinant of forest composition and functional forest composition in specific in the Amazonian landscape because of the differential response of the ecological groups to this form of disturbance both in relation to the type of drought and between the different groups.

ACKNOWLEDGMENT

We would like to thank the Biological dynamics of forest fragment project personnel for kindly allowing access to their permanent sample plots phytodemographic database. This is

publication No.616 in the Biological Dynamics of Forest Fragments Project technical series.

REFERENCES

- [1] D.C.Allen,A.K.Macalady,H.Chenchoumi,D.Bachellet,N.Mcdowell,M.Venier T.Kitzberger, A.Rigling, B.D.Breshers, E.H.Hogg, Gonzalez, R.Fensham, Z. Zhang, J.Castro, N.Demidova, J.H.Lim, G.Allard, S.W.Running, A.Semerci, N.Cobb, "A global overview of drought and heat induced tree mortality reveals emerging climate change risks for forests," *Forest Ecology and Management* ,2010, vol.259,no 4,pp 660-684.
- [2] D.A.Clark, and D.B.Clark,"Life history diversity of canopy and emergent trees in a neotropical rain forest,"1992, *Ecological Monographs*, vol.62, pp 315-344.
- [3] R.Condit, S.P. Hubbell, and R.B. Foster "Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought,"1992,*Ecological Monographs* vol.65, 419-439.
- [4] R.Condit, S. Aguilar, A. Hernandez, R.Perez, S.Lao, G.Angehr, S.P. Hubbell, and R. B.Foster "Tropical forest dynamics across a rainfall gradient and the impact of an El Nino dry season," 2004,*Journal of Tropical Ecology*, vol.20,pp. 51-72.
- [5] A.C.L.da Costa, D.Galbraith,S.Almeida , B.T.T.Portela, M.Da Costa, J.de Athaydes Silva, A.P.Braga, P.H.L.de Goncalves, A.A.R.de Oliveira, R.Fisher, O.L.Phillips, D.L.Metcalf, P.Levy and P.Meir "Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest" 2010, *New Phytologist* vol. pp 187,pp.579-591.
- [6] B.M.J.Engelbrecht, L.S.Comita, R.Condit, T.A.Kursar, M.T.Tyree, B.L. Turner.and S.P. Hubbell "Drought sensitivity shapes species distribution patterns in tropical forests," 2007, *Nature Letters*, vol.447 pp 80-82.
- [7] K.J.Feeley, S.J. Wright, M.N. Nur Supardi, Rahman A. Kassim, and S.J.Davies "Decelerating growth in tropical forest trees" 2010,*Ecology Letters*, vol.10, pp. 461-469.
- [8] S.Gourlet-Fleury, L.B.Lanc, N.P.Piccard, P.S Sist., J.Dick, R.B. Asi, M. Swaine and E.F.Forni "Grouping tree species for predicting mixed tropical forest dynamics: looking for a strategy,"2005, *Ann. For. Sci*, vol.62, pp.785-796.
- [9] D. King, S.J.Davies, M.N. Nur Supadi and S. Tan "Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia,"2005, *Functional Ecology*, vol.19, pp. 445-453.
- [10] D. King, S.J. Davies, and N.S.Md Noor "Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest," 2006, *Forest Ecology and Management*, vol.223, pp. 152-158.
- [11] P.Kohler, T. Ditzer and A. Huth "Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests,"2000, *J. Trop. Ecol.*, vol.16,pp.591-602.
- [12] W.F.Laurance, L.V. Ferreira, J.M. Rankin and S.G. Laurance "Rain forest fragmentation and the dynamics of Amazonian tree communities 1998, *Ecology* vol.79, pp.2032-2040.
- [13] S. Lewis, O. Phillips, D. Sheil, B. Vinceti, T.R. Baker, S. Brown, A.W. Graham, N. Higuchi, D.W. Hilbert, W. Laurance, J. Lejoly, Y. Malhi, A. Monteagudo, P. Nunez-Vargas, S. Bonaventure, M.N. Nur Surpardi, J.W.Terborgh, R.Vazquez-Martinez "Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary" 2004,*Journal of Ecology*, vol.10 pp.1365-2745
- [14] Y.Malhi, T.R.Baker, O.L.Phillips, S.Almeida, E.Alvarez, L.Arroyo, J. Chave, C.I.Czimeczic, A.Di Fiore, N.Higuchi, T.J.Kileen, S.Laurance, W.Laurance, S.Lewis, M. Mercado-Montoya, A.Monteagudo, D.A.Neill, P.Quesada, R. Salomao, J.N.M. Silva, A.Lezama-Torres, R.Vasquez-Martinez, J.Terborgh, B.Vincenti and J. Lloyd "The above-ground coarse woody productivity of 104 Neotropical forest plots,"2004,*Global Change Biology*, vol.10, pp. 563-591.
- [15] D.C. Nepstad, I.M Tohver., D.Ray, P.Moutinho and G.Cardinot "Mortality of large trees and lianas Following experimental drought in an Amazon Forest," 2007, *Ecology*, vol.88, no.9, pp. 2259-2269.
- [16] M.P. Oatham and R. Seepersad "Dynamics of pioneer and primary successional stage trees in a logged Trinidadian tropical rainforest and the influence of drought"2006, *Tropical Ecology*,vol. 47,no.1,pp. 13-26.
- [17] O.L. Phillips., L. E.Aragão, Lewis S. L., J. B.Fisher, J. Lloyd, G. López-González, Y. Malhi, A. Monteagudo , J. Peacock ,C.A. Quesada, G.van der Heijden , S.Almeida , I.Amaral , L. Arroyo , G. Aymard ,T.R. Baker ,O. Bánki , L. Blanc , D. Bonal, P. Brando , J.Chave , Á. C. Alves de

- Oliveira, N. D.Cardozo, C. I.Czimeczik, T. R.Feldpausch, M. Aparecida Freitas, E. Gloor, N. Higuchi, E. Jiménez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A.Neill, D. Nepstad, S. Patiño, M. C. Peñuela, A. Prieto F. Ramírez, M. Schwarz, J. Silva, M. Silveira, A. Sota Thomas, H. ter Steege, J. Stropp, R. Vásquez, P. Zelazowski, E. Alvarez Dávila, S. Andelman, A. Andrade, K. Chao, T. Erwin, A. Di Fiore, C. E. Honorio, H.Keeling, T. J.Killeen, W. F.Laurance, A. Peña Cruz, N. C. A. Pitman, P. Núñez Vargas, H. Ramírez-Angulo, A. Rudas, R. Salamão, N. Silva, J. Terborgh and A. Torres-Lezama "Drought Sensitivity of the Amazon Rainforest," 2009, *Science*, vol.323, pp. 1344-1347.
- [18] L.Poorter, S.J.Wright, H. Paz, D.Ackerly, R. Condit, G. Ibara-Manriquez, K.E. Harms, J.C.Licona, M. Martinez-Ramos, S.G. Mazer, H.C.Muller-Landau, M. Pena-Claros, C.O.Webb, I.J.Wright "Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests," 2008, *Ecology*, vol.89, no.7, pp. 1908-20.
- [19] D.Sheil, D.F.R.P. Burslem and D. Alder, "The interpretation and misinterpretation of mortality rate measures," 1995, *Journal of Ecology*, vol.83, pp. 331-333.
- [20] D. Sheil, and R.M. May. "Mortality and recruitment rate evaluations in heterogeneous tropical forests," 1996, *Journal of Ecology*, vol.84, pp. 91-100.
- [21] Slik J.W.F, "El Nino droughts and their effects on tree species composition and diversity in tropical rain forests,"2004, *Oecologia*, vol.141, pp. 114-120.
- [22] M.D. Swaine and T.C. Whitmore "On the definition of ecological species groups in tropical rain forests," 1988, *Vegetatio*, vol.75 pp. 81-86.
- [23] H.ter Steege, N.Pitman, D.Sabatier, H.Castellanos, P.van der Hout, D.C.Daly M. Silveira, O.Phillips, R.Vasquez, T.van Andel, J.Duivenvoorden, A.A.de Oliveira, R.Ek, R.Lilwah, R.Thomas, J.van Essen, C.Baider, P.Maas, S.Mori, J.Terborgh, P.Núñez Vargaz, H. Mogollón, and W. Morawetz, "A spatial model of tree α -diversity and tree density for the Amazon,"2003, *Biodiversity and Conservation*, vol.12, pp. 2255-2277.
- [24] H.terSteege,N.C.A.Pitman,O.L.Phillips,J.Chave,D.Sabatier,A.Duque,J.F.Molino,M.F.Prevost R.Spichiger, H.Castellanos, P. von Hildebrand and R. Vasquez "Continental-scale patterns of canopy tree composition and function across Amazonia," 2006, *Letters to Nature* vol.443, no.28, pp. 444-447.
- [25] G.Vincent, H.de Foresta and R.Mulia "Co-occurring tree species show contrasting sensitivity to ENSO-related droughts in planted dipterocarp forests," 2009, *Forest Ecology and Management*, vol. 258, pp.1316-1322.
- [26] C.Whitmore"Forty Years of Rain Forest Ecology: 1948-1988 in Perspective,"1989, *Geojournal*, vol.19 pp. 347-360.
- [27] B.Williamson,W.F. Laurance, A.Oliveira, Delamonica P., C. Gauscon, T. Lovejoy and L. Pohl "Amazonian tree mortality during the 1997 El Nino drought,"2000,*Conservation Biology*, vol.14,no.5,pp. 1538-1542.