

**University of São Paulo
"Luiz de Queiroz" College of Agriculture
Center for Nuclear Energy in Agriculture**

**How Amazon trees growth are affected and react to forest fragmentation
and climate changes? A dendrochronology approach**

Alci Albiero Júnior

Thesis presented to obtain the degree of Doctor in
Science. Area: Applied Ecology

**Piracicaba
2019**

Alci Albiero Júnior
Biologist, Master in Botany

How Amazon trees growth are affected and react to forest fragmentation and climate changes? A dendrochronology approach

Advisor:
Prof. Dr. **MARIO TOMMASIELLO FILHO**

Thesis presented to obtain the degree of Doctor in
Science. Area: Applied Ecology

Piracicaba
2019

Dados Internacionais de Catalogação na Publicação
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP

Albiero Júnior, Alci

How Amazon trees growth are affected and react to forest fragmentation and climate changes? A dendrochronology approach / Alci Albiero Júnior. - - Piracicaba, 2019.

125 p.

Tese (Doutorado) - - USP / Escola Superior de Agricultura "Luiz de Queiroz". Centro de Energia Nuclear na Agricultura.

1. Dendroecologia 2. Dendroclimatologia 3. Perda de habitat 4. Dossel
5. Sub-dossel 6. Projeto Dinâmica Biológica de Fragmentos Florestais I.
Título

This doctoral thesis is dedicated to trees

ACKNOWLEDGEMENTS

First of all I thank my family, my father Alci, my mother Leliane and my sisters Larissa and Maria Paula for their love and support throughout my life. This walk was much easier with you by my side.

I grateful the encounters with amazing people that academic life has given me, fundamental to my growth and learning.

My advisor Dr. Mario Tommasiello Filho, for his support, opportunities and liberty during the four years of doctorate.

My co-advisor Dr. José Luiz Campana Camargo, for believe and fully engaging with the work proposal, making elementary contributions at all stages. I also thank for your suport during my stay in Manaus/AM.

To Dr. Fidel Alejandro Roig, for his presence and guidance on tree rings studies. In addition to the great opportunity to develop part of my studies under his supervision at IANIGLA/Mendoza/Argentina.

To Dr. Jochen Schöngart for his support and suggestions in defining the studied species and interpreting climate analysis.

To Dr. Alejandro Venegas González for his friendship and contributions in the papers publications.

To Dr. Renan Mercuri Pinto for his valuable contributions in structural equation analysis.

To all friends of Wood Anatomy and Tree-Ring Laboratory, Aparecido Candido, Maria Aparecida, Fernanda Trislitz, Mariana Pires, Luiz Santini Jr, Claudio Anholetto Jr, Luciana Karla, Roger Legoas, Daigard Ricardo, Manolo Trindade, Alinne Santos, Francisco de Marques, Júlia Lôbo, Alessandra Voigt and Pedro Vieira for the shared moments.

To Applied Ecology/ESALQ/CENA/USP Postgraduate Program, for the opportunity to develop my doctoral thesis.

To Brazilian Federal Agency for the Improvement of Higher Education Personnel (CAPES) for the Ph.D. scholarship support.

This work was funded by the Rufford Small Grant for Nature Conservation (RSGA application 18762-1), BDFFP's Thomas Lovejoy research fellowship program and conducted during a scholarship supported by the International Cooperation Program CAPES/PVE (process: 88887.127558/2016-00) at Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Mendoza, Argentina.

As árvores são fáceis de achar
Ficam plantadas no chão
Mamam do céu pelas folhas
E pela terra
Também bebem água
Cantam no vento
E recebem a chuva de galhos abertos
Há as que dão frutas
E as que dão frutos
As de copa larga
E as que habitam esquilos
As que chovem depois da chuva
As cabeludas, as mais jovens mudas
As árvores ficam paradas
Uma a uma enfileiradas
Na alameda
Crescem pra cima como as pessoas
Mas nunca se deitam
O céu aceitam
Crescem como as pessoas
Mas não são soltas nos passos
São maiores, mas
Ocupam menos espaço
Árvore da vida
Árvore querida
Perdão pelo coração
Que eu desenhei em você
Com o nome do meu amor.

Arnaldo Antunes / Jorge Ben Jor

SUMMARY

RESUMO	8
ABSTRACT	10
LIST OF FIGURES	11
LIST OF TABLES	14
GENERAL INTRODUCTION	15
References	17
OBJECTIVES	21
Chapter 1	23
WHAT IS THE TEMPORAL EXTENSION OF EDGE EFFECTS ON TREE GROWTH DYNAMICS? A DENDROCHRONOLOGICAL APPROACH MODEL USING <i>Scleronema micranthum</i> (DUCKE) DUCKE TREES OF A FRAGMENTED FOREST IN THE CENTRAL AMAZON	23
Abstract	23
Introduction	24
Materials and Methods	26
Study and sampling areas	26
<i>Scleronema micranthum</i> tree-ring analysis	27
Site growth patterns	28
Disturbance analysis	29
Results	29
Tree-rings chronologies of <i>Scleronema micranthum</i>	29
Site growth patterns	31
Disturbance analysis	35
Discussion	37
Tree-ring chronologies of <i>Scleronema micranthum</i> trees	37
Site growth patterns	37
Disturbance analysis	39
Conclusions	40
Acknowledgements	41
References	41
Chapter 2	49

AMAZONIAN TREES SHOW INCREASED EDGE EFFECTS DUE TO ATLANTIC OCEAN WARMING AND NORTHWARD DISPLACEMENT OF THE INTERTROPICAL CONVERGENCE ZONE SINCE 1980	49
Abstract.....	49
Introduction	50
Materials and Methods	52
Study and sampling areas	52
Tree-ring analyses of <i>Scleronema micranthum</i>	53
Growth-climate analyses	54
Results	56
Tree-rings chronologies of <i>Scleronema micranthum</i>	56
Climate-growth analyses	58
Discussion.....	64
Conclusion.....	67
Acknowledgements	67
References	68
Chapter 3	75
NOT EVERYTHING IS SO BAD: TREE GROWTH UNDER CANOPY OF TERRA FIRME FOREST IN CENTRAL AMAZONIA IS FAVORED AFTER FOREST FRAGMENTATION	75
Abstract.....	75
Introduction	76
Materials and Methods	78
Study and sampling areas	78
Theobroma sylvestre tree-ring analysis	79
Site growth patterns	80
Disturbance analysis	81
Results	82
Tree-ring chronologies of <i>Theobroma sylvestre</i>	82
Site growth patterns	84
Disturbance analysis	85
Discussion.....	89
Conclusion.....	92
Acknowledgements	93

References	93
Chapter 4	101
TREES UNDER CANOPY OF TERRA FIRME FOREST IN CENTRAL AMAZONIA ARE MORE TOLERANT TO LOCAL AND LARGE-SCALE CLIMATE CHANGES.....	101
Abstract	101
Introduction.....	101
Materials and Methods.....	103
Study and sampling areas.....	103
Theobroma sylvestre tree-ring analysis	104
Growth-climate analyses.....	105
Results.....	106
Tree-ring chronologies of <i>Theobroma sylvestre</i>	106
Growth-climate analyses.....	109
Discussion	113
Conclusion	117
References	118
OVERALL CONCLUSIONS	125

RESUMO

Como as árvores da Amazônia são afetadas e reagem à fragmentação florestal e mudanças climáticas? Uma abordagem dendrocronológica

As árvores são consideradas elementos fundamentais das florestas tropicais, desempenhando papéis centrais na manutenção e equilíbrio dos Ecossistemas a que estão associadas e no fornecimento de serviços ambientais indispensáveis para o bem-estar humano. Por serem seres sésseis e longevos, se tornam excelente bioindicadores temporais das alterações ambientais pretéritas e presentes a que são expostas ao longo de suas vidas. Atualmente, a conservação da maior floresta tropical do mundo está fortemente ameaçada pelos avanços nas taxas de desmatamento e mudanças climáticas do Antropoceno. Nesse contexto, através de uma perspectiva dendrocronológica, o presente estudo teve como objetivo avaliar como árvores ocupando diferentes perfis verticais da floresta de *terra firme* na Amazônia central brasileira são afetadas por efeitos de borda e mudanças climáticas e reagem a esses fenômenos ao longo da vida. Através dos anéis de crescimento revelamos que árvores de *Scleronema micranthum* (Ducke) Ducke (Malvaceae) localizadas no dossel florestal são mais sensíveis aos efeitos de borda e mudanças climáticas, apresentando redução de 18% em suas taxas de crescimento durante os primeiros 10 anos de fragmentação. Resultado oposto aos observados para árvores de *Theobroma sylvestre* Mart. (Malvaceae) localizadas nos perfis verticais inferiores da floresta que aumentaram suas taxas de crescimento em aproximadamente 6% durante os primeiros 20 anos de fragmentação. Confirmando que mudanças climáticas locais e estruturais provocadas pelos efeitos de borda e alterações climáticas de larga escala relacionadas principalmente ao aquecimento e resfriamento dos oceanos exercem diferenças contrastantes na dinâmica de crescimento de árvores dependendo de sua posição no perfil vertical da floresta. Portanto, destacamos a relevância dos anéis de crescimento como bioindicadores da fragmentação florestal e mudanças climáticas locais e de larga escala a que as árvores são expostas durante suas vidas. Fornecendo novas perspectivas sobre a capacidade de resiliência das árvores da Amazônia, corroborando com práticas de manejo e restauração florestal em cenários futuros de fragmentação e aquecimento global.

Palavras-chave: Dendroecologia, Dendroclimatologia, Perda de habitat, Dossel, Sub-dossel, Projeto Dinâmica Biológica de Fragmentos Florestais

ABSTRACT

How Amazon trees growth are affected and react to forest fragmentation and climate changes? A dendrochronology approach

Trees are considered key elements of tropical forests, playing central roles in maintaining and balancing of the ecosystems with which they are associated and in providing environmental services that are indispensable for human well-being. Because they are sessile and long-lived beings, they become excellent temporal bioindicators of past and present environmental changes to which they are exposed throughout their lives. Currently, the conservation of the world's largest rainforest is strongly threatened by advances in deforestation rates and the Anthropocene climate changes. In this context, through a dendrochronological perspective, the present study aimed to evaluate how trees occupying different vertical profiles of the *terra firme* forest in central Brazilian Amazonia are affected by edge effects and climate change and react to these phenomena during their lifetime. Through tree rings we reveal that *Scleronema micranthum* (Ducke) Ducke (Malvaceae) trees located in the forest canopy are more sensitive to edge effects and climate change, showing an 18% reduction in their growth rates during the first 10 years of forest fragmentation. Opposite results to those observed for *Theobroma sylvestre* Mart. (Malvaceae) trees located under forest canopy that increased their growth rates by approximately 6% during the first 20 years of fragmentation. Confirming that structural and climate changes caused by edge effects and large-scale climate changes mainly related to oceans warming and cooling exert contrasting differences in tree growth dynamics depending on their position in the vertical profile of the forest. Therefore, we highlight the relevance of tree rings as bioindicators of forest fragmentation and local and large-scale climate change to which trees are exposed during their lives. Providing new perspectives on Amazonian trees resilience, corroborating with forest management and restoration practices in future scenarios of fragmentation and global warming.

Keywords: Dendroecology, Dendroclimatology, Habitat loss, Canopy, Sub-canopy, Biological Dynamics of Forest Fragments Project

LIST OF FIGURES

Figure 1. a) <i>Scleronema micranthum</i> tree on edge at Biological Dynamics of Forest Fragments Project site; b) Macro and c) microscopic images of the transverse wood section	30
Figure 2. Residual tree-ring chronology of <i>Scleronema micranthum</i> trees for Edge (a) and Interior (b) locations in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.	30
Figure 3. Principal Component Analysis described by BAI series of <i>Scleronema micranthum</i> trees located close to the edge and in the interior of the forest in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.....	33
Figure 4. Dominant basal area increment index patterns of <i>Scleronema micranthum</i> trees located close to the edge and in the interior of the forest in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.	34
Figure 5. Release events in <i>Scleronema micranthum</i> trees close to the forest edge and in the interior of the forest or far from the edge in <i>terra firme</i> forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.....	36
Figure 6. Minimum, mean and maximum temperatures and mean monthly precipitation in Central Amazonia from 1941 to 2014	52
Figure 7. Location of the two study sites at the Biological Dynamics of Forest Fragments Project (BDFFP) in <i>terra firme</i> forests of Central Amazonia.	53
Figure 8. a) <i>Scleronema micranthum</i> tree at the forest edge at the Biological Dynamics of Forest Fragments Project site; b) macroscopic, and c) microscopic images of the transverse wood section.....	57
Figure 9. Residual tree-ring chronologies of <i>Scleronema micranthum</i> at the forest edge and in intact <i>terra firme</i> forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.....	57
Figure 10. Dominant basal area increment index patterns of <i>Scleronema micranthum</i> trees located close to the edge and in the interior of the forest in <i>terra firme</i> forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	59
Figure 11. Spatial correlations between the Atlantic sea surface temperature and the basal area increment of <i>Scleronema micranthum</i> trees not exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	60

Figure 12. Spatial correlations between the Atlantic sea surface temperature and the basal area increment of <i>Scleronema micranthum</i> trees exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	61
Figure 13. Structural Equation Model of climate-growth relationships for trees not exposed and exposed to edge effects for the periods before, during and after the dry season.	64
Figure 14. Location of the two study sites of terra firme forests at the Biological Dynamics of Forest Fragments Project (BDFFP) in Central Amazonia.	79
Figure 15. A) <i>Theobroma sylvestre</i> tree in the edge of the reserve at the Biological Dynamics of Forest Fragments Project site; B) Macro and C) Microscopic images of the transverse wood section.	83
Figure 16. Residual tree-ring chronology of <i>Theobroma sylvestre</i> trees for Edge and Interior locations in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	83
Figure 17. Principal Component Analysis described by BAI series of <i>Theobroma sylvestre</i> trees located close to the edge and into the interior of the forest in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	87
Figure 18. Dominant basal area increment index patterns of <i>Theobroma sylvestre</i> trees located close to the edge and in the interior of the forest in <i>terra firme</i> forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	88
Figure 19. Release events in <i>Theobroma sylvestre</i> trees close to the forest edge and into the interior of the forest or far from the edge in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	89
Figure 20. Location of the two study sites at the Biological Dynamics of Forest Fragments Project (BDFFP) in <i>terra firme</i> forests of Central Amazonia.	104
Figure 21. A) <i>Theobroma sylvestre</i> tree in the edge at Biological Dynamics of Forest Fragments Project site; B) Macro and C) microscopic images of the transverse wood section.	107
Figure 22. Residual tree-ring chronology of <i>Theobroma sylvestre</i> trees for Edge (a) and Interior (b) locations in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.	108

- Figure 23.** Dominant basal area increment index patterns of *Theobroma sylvestre* trees located close to the edge and in the interior of the forest in *terra firme* forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.. 109
- Figure 24.** Spatial correlations between the Atlantic sea surface temperature and the basal area increment of *Theobroma sylvestre* trees not exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia 111
- Figure 25.** Spatial correlations between the Atlantic sea surface temperature and the basal area increment of *Theobroma sylvestre* trees exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia 112
- Figure 26.** Correlation analysis constructed through Pearson correlation coefficient, between historical series of basal area increment rates of trees exposed to edge effects, basal area increment rates of trees not exposed to edge effects, precipitation, South Atlantic sea surface temperature; North Atlantic sea surface temperature; Pacific decadal oscillation and Pacific sea surface temperature, before the dry season, during the dry season and after the dry season. 113

LIST OF TABLES

Table 1. Descriptive statistics of the chronologies of <i>Scleronema micranthum</i> trees located close to the edge and in the interior of the reserve at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.....	31
Table 2. Age and diameter at breast height of <i>Scleronema micranthum</i> trees at edge and interior sites in terra firme forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia selected for growth pattern analyzes.	31
Table 3. Basal area increments of <i>Scleronema micranthum</i> trees located close to the edge and in the interior of the forest during a common growth time period in <i>terra firme</i> forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.	35
Table 4. Descriptive statistics of tree-ring chronologies of <i>Scleronema micranthum</i> located close to the edge and in the interior of the reserves at the Biological Dynamics of Forest Fragments Project in Central Amazonia.....	58
Table 5. Age and diameter at breast height of <i>Scleronema micranthum</i> trees at edge and interior of <i>terra firme</i> forests at the Biological Dynamics of Forest Fragments Project in Central Amazonia selected for growth pattern analyses.....	58
Table 6. Descriptive statistics of the chronologies of <i>Theobroma sylvestre</i> trees located close to the edge and in the interior of the forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.....	84
Table 7. Age and diameter at breast height of <i>Theobroma sylvestre</i> trees at edge and interior sites in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia selected for growth pattern analyzes.	84
Table 8. Basal area increments of <i>Theobroma sylvestre</i> trees located close to the edge and in the interior of the forest during a common growth time period in <i>terra firme</i> forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. ..	88
Table 9. Descriptive statistics of the chronologies of <i>Theobroma sylvestre</i> trees located close to the edge and in the interior of the forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.....	108
Table 10. Age and diameter at breast height of <i>Theobroma sylvestre</i> trees at edge and interior sites in <i>terra firme</i> type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia selected for growth pattern analyzes.	109

GENERAL INTRODUCTION

The Amazonian forest view as a pristine nature before European colonization is currently very simplistic and romanticized. Recent studies and archaeological, paleoenvironmental and ecological discoveries highlight that the world's largest rainforest already presented landscape changes due to human action during pre-Columbian times (Heckenberger et al., 2003; Clement et al., 2015; Levis et al., 2018; Andrade et al., 2019).

The impact of *Homo sapiens* on biological equilibrium dates from its appearance on earth, and despite not having many tools and high population density for major landscape transformations, primitive human was already using a very powerful instrument capable of major environmental modifications, the fire (Dorst, 1973; Dean, 1997). The Amazon areas covered by *terra preta*, soils of anthropic origin, resulting from the accumulation of charred organic waste, confirm the strong relationship of pre-Columbian indigenous peoples with the use of fire (Neves et al., 2003).

In this sense, the relationship between humans and the environment depends heavily on the group in question, considering that cultural, technological, wealth and political power differences reflect the environmental impact of their activities (Fearnside, 2003).

From the eighteenth century onwards, the massive population density growth associated with technological advances of a capitalist world, favored the unprecedented impact of human activities on the planet, making human action for the first time in history able to produce geological forces (e.g. land use changes, deforestation, fossil fuel burning) that cause profound environmental changes (Crutzen, 2006).

Among these profound environmental changes, we can highlight the forest fragmentation and climate changes. Considering that currently, it is estimated that there are more than 50 million tropical forest fragments, comprising an area > 1.5 billion ha, with 50 million km of edge (Brinck et al., 2017). And future climate scenarios projections reveal a global temperatures increase in response to increase burning of fossil fuels by the human activities (Intergovernmental Panel on Climate Change 2019).

According to Haddad et al (2015), the outcome of human impact on forest fragmentation can produce three fundamental “debts”: the “extinction debt”, where loss of forest species takes more than 10 years to reach 50% of previous mature areas; the “immigration lag”, where fewer species arrive in remote areas; and “ecosystem function debt”, described as delayed changes in nutrient cycling and to plant and consumer biomass.

Numerous other “debts” able to influence human well-being can also be attributed to climate changes: directly affecting metabolic and developmental rates in many plants, altering

fundamental processes such as photosynthesis, respiration, growth and tissue composition (Hughes, 2000); increasing the number of extreme drought and flood events (Yoon and Zeng, 2010; Marengo et al., 2012; Barichivich et al., 2018; Espinoza et al., 2019); intensifying psychological (e.g. concern and uncertainty about future risks) and psychosocial (e.g. migration and climate-related conflicts) impacts (Doherty and Clayton, 2011); and changing the global production of major crops (Lobell and Field, 2007). That is, the future of human well-being will depend on its current action on the environment.

Currently the increase of Brazilian Amazonian forest deforestation by approximately 88% compared to 2018 (INPE, 2019), and the ongoing potential increases of legal deforestation after Brazilian Forest Act revision, that favors the reduction size of the legal reserves for nature protection from 80% to 50% in Amazonian private properties (Freitas et al., 2018). Together with the promises and actions of the Brazil's new president, that threaten Brazilian Amazonian forest and the traditional people who inhabit it (Ferrante and Fearnside, 2019) and the tipping point of 20–25% in deforestation rates for the Amazon ecosystem to become a non-forest system (Lovejoy and Nobre, 2018). Highlight the urgency for studies that evaluate how Amazonian forest ecosystems and their services recover after human disturbances.

In these sense, recognizing the key role of trees in conservation and supply of essential environmental services provide by Amazon forest, being a relevant source of water vapor for the entire climate system (Nobre et al., 2009a), able to release 20 trillion liters of water a day (Nobre, 2014). It also contributes with ~17% of total global freshwater input to the oceans (Callede et al., 2010) and to the energy balance and climate maintenance of the planet (Hilker et al., 2014; Wang and Fu, 2007). Indispensable for the global carbon cycle (Malhi et al., 2006; Saatchi et al., 2007) through photosynthetic fixation of 17% of the terrestrial carbon biomass (Fauset et al., 2015).

Researches that seek evaluate how trees species in the world's largest hydrographic basin are affected and respond to forest fragmentation and climate change along their life's cycle will be indispensable to understanding the Amazon forest resilience. Knowledge that benefit Amazon forest management and restoration practices in current scenarios of forest fragmentation and global warming.

Evaluate how tree growth is influenced by the environment is not necessarily contemporary, Leonardo da Vinci already recognized them in the fifteenth century by measuring the width of tree rings. However, only from the twentieth century that dendrochronology (*dendron*, wood; *chronos*, time; and *logus*, study) was consolidated as a

modern science by the North American Andrew E. Douglas in looking at the relationships between solar activity cycles and the earth's climate with tree rings (Schweingruber, 1988). By adding a long-term perspective, dendrochronology is an effective tool to evaluate how forest fragmentation and climate changes influence tree growth dynamics throughout their life's cycle, reflecting the effect of biotic and abiotic factors on the periodicity of cambial activity (Callado et al., 2014).

Although many dendrochronological studies conducted in tropical forests have already revealed important results of the climatic influence on tree growth dynamics (Vetter and Botosso, 1989a,b; Worbes, 2002; Dünisch, 2005; Schongart et al., 2006; Brienen et al., 2010; Granato-Souza et al., 2018; Venegas-González et al., 2018; Fontana et al., 2018). Until now, few have used growth rings as bioindicators of tropical forest fragmentation and edge effects (Godoy-Veiga et al., 2018; Albiero-Júnior et al., 2019a, 2019b).

References

- Albiero-Júnior, A., Camargo, J.L.C., Roig, F.A., Schöngart, J., Pinto, R.M., Venegas-González, A., Tomazello-Filho, M. Amazonian trees show increased edge effects due to Atlantic Ocean warming and northward displacement of the Intertropical Convergence Zone since 1980. *Sci. Total Environ*, v.693, p.133515, 2019a.
- Albiero-Júnior, A., Venegas-González, A., Botosso, P.C., Roig, F.A., Camargo, J.L.C., Tomazello-Filho, M. What is the temporal extension of edge effects on tree growth dynamics? A dendrochronological approach model using *Scleronema micranthum* (Ducke) Ducke trees of a fragmented forest in the Central Amazon. *Ecol. Indic*, v.101, p. 133–142, 2019b.
- Andrade, V.L.C., Flores, B.M., Levis, C., Clement, C.R., Roberts, P., Schöngart, J. Growth rings of Brazil nut trees (*Bertholletia excelsa*) as a living record of historical human disturbance in Central Amazonia. *PLoS One*, v. 14, p.1-18, 2019.
- Barichivich, J., Gloor, E., Peylin, P., Brienen, R.J.W., Schöngart, J., Espinoza, J.C., Pattanayak, K.C. Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. *Sci. Adv*, v. 4, p. 85-87, 2018.
- Brienen, R J W, Zuidema, P.A., Martinez-Ramos, M. Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions. *Oecologia*, v. 163, p. 485–496, 2010.

- Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., De Paula, M.D., Pütz, S., Sexton, J.O., Song, D., Huth, A. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nat. Commun.*, v. 8, p.1-6, 2017.
- Callado, C.H., Vasconcellos, T.J., Costa, M.S., Barros, C.F., Roig, F.A., Tomazello-Filho, M. Studies on cambial activity: advances and challenges in the knowledge of growth dynamics of Brazilian woody species. *An. Acad. Bras. Cienc.*, v. 86, p. 277–284, 2014.
- Callede, J., Cochonneau, G., Vieira Alves, F., Guyot, J.-L., Santos Guimaraes, V., De Oliveira, E. The river amazon water contribution to the atlantic Ocean. *Rev. des Sci. l'eau*, v. 23, p.247-273, 2010.
- Clement, C.R., Denevan, W.M., Heckenberger, M.J., Junqueira, A.B., Neves, E.G., Teixeira, W.G., Woods, W.I. The domestication of Amazonia before European conquest. *Proc. R. Soc. B Biol. Sci.*, v. 282, p.1-9, 2015.
- Crutzen, P.J. The “anthropocene,” in: *Earth System Science in the Anthropocene*. Springer, pp. 13–18, 2006.
- Dean, W. *A ferro e fogo: a história e a devastação da Mata Atlântica brasileira*. Companhia das Letras, 1996.
- Doherty, T.J., Clayton, S. The psychological impacts of global climate change. *Am. Psychol.*, v. 66, p. 265-297, 2011.
- Dorst, J. *Antes que a natureza morra*. Edgard Blucher, 1973. p.394.
- Dünisch, O. Influence of the El-niño southern oscillation on cambial growth of *Cedrela fissilis* Vell. in tropical and subtropical Brazil. *J. Appl. Bot. food Qual.* v. 79, p. 5–11, 2005.
- Espinoza, J.C., Ronchail, J., Marengo, J.A., Segura, H. Contrasting North–South changes in Amazon wet-day and dry-day frequency and related atmospheric features (1981–2017). *Clim. Dyn.*, v.53, p. 1–18, 2019.
- Fauset, S., Johnson, M.O., Gloor, M., Baker, T.R., Monteagudo, A., Brienen, R.J.W., Feldpausch, T.R., Lopez-Gonzalez, G., Malhi, Y., Ter Steege, H. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.*, v. 6, p. 7857-7866, 2015.
- Fearnside, P.M. *A floresta amazônica nas mudanças globais*. INPA, Manaus, 2003, p.145.
- Ferrante, L., Fearnside, P.M. Brazil’s new president and ‘ruralists’ threaten Amazonia’s environment, traditional peoples and the global climate. *Environ. Conserv.*, v.9, p. 1–3, 2019.

- Fontana, C., Pérez-de-Lis, G., Nabais, C., Lousada, J.L.P.C., Olmedo, G.M., Botosso, P.C., Oliveira, J.M. Climatic signal in growth-rings of *Copaifera lucens*: an endemic species of a Brazilian Atlantic Forest hotspot, southeastern Brazil. *Dendrochronologia*, v. 50, p. 23–32, 2018.
- Freitas, F.L.M., Sparovek, G., Berndes, G., Persson, U.M., Englund, O., Barretto, A., Mörtberg, U. Potential increase of legal deforestation in Brazilian Amazon after Forest Act revision. *Nat. Sustain*, v.1, p. 665-670, 2018.
- Godoy-Veiga, M., Ceccantini, G., Pitsch, P., Krottenthaler, S., Anhuf, D., Locosselli, G.M. Shadows of the edge effects for tropical emergent trees: the impact of lianas on the growth of *Aspidosperma polyneuron*. *Trees*, v.32, p. 1073–1082, 2018.
- Granato-Souza, D., Stahle, D.W., Barbosa, A.C., Feng, S., Torbenson, M.C.A., de Assis Pereira, G., Schöngart, J., Barbosa, J.P., Griffin, D. Tree rings and rainfall in the equatorial Amazon. *Clim. Dyn*, v. 52, p. 1857–1869, 2018.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Sci. Adv*, v.1, p. 1-9, 2015.
- Heckenberger, M.J., Kuikuro, A., Kuikuro, U.T., Russell, J.C., Schmidt, M., Fausto, C., Franchetto, B. Amazonia 1492: pristine forest or cultural parkland? *Science* v.301, p. 1710–1714, 2003.
- Hilker, T., Lyapustin, A.I., Tucker, C.J., Hall, F.G., Myneni, R.B., Wang, Y., Bi, J., de Moura, Y.M., Sellers, P.J. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proc. Natl. Acad. Sci*, v. 111, p. 16041–16046, 2014.
- Hughes, L. Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol*, v. 15, p. 56–61, 2000.
- INPE. Satellite-based monitoring of deforestation of the Amazon forest/PRODES “Monitoramento da floresta amazônica brasileira por satélite”, 2019.
- Levis, C., Flores, B.M., Moreira, P.A., Luize, B.G., Alves, R.P., Franco-Moraes, J., Lins, J., Konings, E., Peña-Claros, M., Bongers, F. How people domesticated Amazonian forests. *Front. Ecol. Evol*, v. 5, p. 171, 2018.
- Lobell, D.B., Field, C.B. Global scale climate–crop yield relationships and the impacts of recent warming. *Environ. Res. Lett*, v. 2, p. 14002, 2007.
- Lovejoy, T.E., Nobre, C. Amazon Tipping Point. *Science Advances*, v. 4, p. 2340, 2018.

- Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Glob. Chang. Biol.*, v. 12, p. 1107–1138, 2006.
- Marengo, J.A., Tomasella, J., Soares, W.R., Alves, L.M., Nobre, C.A. Extreme climatic events in the Amazon basin. *Theor. Appl. Climatol.*, v. 107, p. 73–85, 2012.
- Neves, E.G., Petersen, J.B., Bartone, R.N., Da Silva, C.A. Historical and socio-cultural origins of Amazonian dark earth, in: *Amazonian Dark Earths*. Springer, 2003. p. 29–50.
- Nobre, A.D. O futuro climático da Amazônia-relatório de avaliação científica. *Articul. Reg. Amaz.* São José dos Campos CPTEC/INPE.2014
- Nobre, C.A., Marengo, J.A., Artaxo, P. Understanding the climate of Amazonia: Progress from LBA. *Washingt. DC Am. Geophys. Union Geophys. Monogr. Ser.* v. 186, p. 145–147, 2009a.
- Saatchi, S.S., Houghton, R.A., Dos Santos Alvala, R.C., Soares, J.V., Yu, Y. Distribution of aboveground live biomass in the Amazon basin. *Glob. Chang. Biol.*, v. 13, p. 816–837, 2007.
- Schongart, J., Orthmann, B., Hennenberg, K.J., Porembski, S., Worbes, M. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. *Glob. Chang. Biol.*, v. 12, p. 1139–1150, 2006.
- Schweingruber, F.H. *Tree rings*. Springer Science & Business Media.1988
- Venegas-González, A., Roig, F.A., Lisi, C.S., Albiero-Junior, A., Alvares, C.A., Tomazello-Filho, M. Drought and climate change incidence on hotspot Cedrela forests from the Mata Atlântica biome in southeastern Brazil. *Glob. Ecol. Conserv.*, v. 15, p.408-420, 2018.
- Vetter, Roland E, Botosso, P.C. El Niño may affect growth behaviour of Amazonian trees. *GeoJournal*, v. 19, p. 419–421, 1989a.
- Vetter, R E, Botosso, P.C. Remarks on age and growth-rate determination of amazonian trees. *Iawa Bull*, v. 10, p. 133–145, 1989b.
- Wang, H., Fu, R. The influence of Amazon rainfall on the Atlantic ITCZ through convectively coupled Kelvin waves. *J. Clim.*, v. 20, p. 1188–1201, 2007.
- Worbes, M. One hundred years of tree-ring research in the tropics - A brief history and an outlook to future challenges. *Dendrochronologia*, v. 20, p. 217-231, 2002.
- Yoon, J.-H., Zeng, N. An Atlantic influence on Amazon rainfall. *Clim. Dyn.*, v. 34, p. 249–264, 2010.

OBJECTIVES

The present doctoral thesis aims to reveal through a dendrochronological perspective, using tree rings as bioindicators, how trees occupying different vertical profiles of the *terra firme* forest in central Brazilian Amazonian are affected by forest fragmentation and climate changes and react to these phenomena during their life. Through this work we hope to better understand how the current and future scenario of forest fragmentation and climate change may modify Amazon trees growth dynamics and resilience.

This thesis is structured and presented through four chapters. Each chapter represents an independent scientific article, although integrated with the general aims of the study.

The first chapter evaluates how forest fragmentation and edge effects influence tree growth dynamics occupying the Amazon forest canopy and was published in the Ecological Indicators journal.

- I) Albiero-Júnior, A., Venegas-González, A., Botosso, P.C., Roig, F.A., Camargo, J.L.C., Tomazello-Filho, M., 2019. **What is the temporal extension of edge effects on tree growth dynamics? A dendrochronological approach model using *Scleronema micranthum* (Ducke) Ducke trees of a fragmented forest in the Central Amazon.** Ecol. Indic. 101, 133–142

The second chapter assesses how local and large-scale climate changes influence tree growth dynamics occupying the Amazon forest canopy and was published in the Science of the Total Environment journal.

- II) Albiero-Júnior, A., Camargo, J.L.C., Roig, F.A., Schöngart, J., Pinto, R.M., Venegas-González, A., Tomazello-Filho, M., 2019. **Amazonian trees show increased edge effects due to Atlantic Ocean warming and northward displacement of the Intertropical Convergence Zone since 1980.** Sci. Total Environ. 693, 133515.

The third chapter assesses how forest fragmentation and edge effects influence tree growth dynamics occupying the lower and intermediate vertical profile of Amazon forest and was submitted to Journal of Ecology.

- III)** Albiero-Júnior, A., Camargo, J.L.C., Roig, F.A., Venegas-González, A., Tomazello-Filho. **Not everything is so bad: tree growth under canopy of *terra firme* forest in Central Amazonia is favored after forest fragmentation.** Submitted to Journal of Ecology.

The fourth chapter assesses how local and large-scale climate changes influence tree growth dynamics occupying the lower and intermediate vertical profile of Amazon forest.

- IV)** **Trees under canopy of terra firme forest in Central Amazonia are more tolerant to local and large-scale climate changes**

Chapter 1

WHAT IS THE TEMPORAL EXTENSION OF EDGE EFFECTS ON TREE GROWTH DYNAMICS? A DENDROCHRONOLOGICAL APPROACH MODEL USING *Scleronema micranthum* (Ducke) DUCKE TREES OF A FRAGMENTED FOREST IN THE CENTRAL AMAZON

Published in the journal: Ecological Indicators, v.101, p. 133–142, 2019.

Alci Albiero-Júnior^a; Alejandro Venegas-González^b; Paulo Cesar Botosso^c; Fidel Roig Juñent^d; José Luís Campana Camargo^e; Mario Tomazello-Filho^a

^aUniversity of São Paulo, Luiz de Queiroz College of Agriculture, Department of forest Sciences, Wood Anatomy and Tree-Ring Laboratory, Av. Pádua Dias 11, P.O. Box 9, 13418-900 Piracicaba, SP, Brazil.

^bFacultad de Ciencias, Escuela de Ingeniería Forestal, Universidad Mayor, Camino La Pirámide 5750, Huechuraba, Santiago, Chile.

^cBrazilian Agricultural Research Corporation (Embrapa), National Forest Research Center, Colombo, Paraná, Brazil.

^dLaboratorio de Dendrocronología e Historia Ambiental, IANIGLA, CCT CONICET Mendoza, CC 330, M5502IRA, Argentina.

^eBiological Dynamics of Forest Fragment Project (BDFFP), Manaus, AM, Brazil.

***Corresponding author:** Telephone +55 19 998798043;

albierojunior@usp.br;junioralbiero@hotmail.com

Abstract

Although the Amazon Forest comprises the world's largest rainforest, providing fundamental ecosystem services to human well-being, vicissitudes imposed by deforestation, climate change, widespread use of fire and development of new infrastructure make the region critically vulnerable to the consequences of the creation of new forest edges. In this forest fragmentation scenario, temporal assessment of edge effects influences throughout the life of the trees become necessary for a better understanding of how species are affected and react when exposed to altered environments. In this study, we evaluated the temporal influence of the edge effect on the growth dynamics of *Scleronema micranthum* (Ducke) Ducke by tree-ring analysis based on basal area increment and release events. This species is one of the most frequent tree species of *terra firme* type of forest in Central Amazonia at the Biological Dynamics of Forest Fragment Project (BDFFP) study sites. The results showed

that edge effects changed the growth dynamics of the trees for at least 10 years after the disturbance, inducing an 18% reduction in tree growth during this period, and records of increased release events. We concluded that growth rings of edge trees are a valuable bioindicators for evaluating the temporal extent of edge effects, and therefore, they must be considered as relevant ecological indicators of historical environmental changes and forest fragmentation, promoting new insights into the resilience ability of trees when exposed to forest fragmentation processes.

Keywords: Dendroecology; Forest fragmentation; Release event; Basal area increment; BDFFP

Introduction

Amazonia comprises the world's largest rainforest (Wesselingh et al., 2010) providing fundamental ecosystem services to human well-being through supply of essential products and materials, control and support of environmental conditions and the provision of cultural and aesthetic benefits (Millenium Ecosystem Assessment, 2003). However, currently, consequences imposed by deforestation, climate change and widespread use of fire may transform the eastern, southern and central Amazon ecosystem into a non-forest system if deforestation areas cross a tipping point of 20-25% of the region (Lovejoy and Nobre, 2018). In this forest fragmentation scenario, essential ecosystem services provided by trees such as the storage of 60% of the total global forest biomass (Pan et al., 2011), nutrient, carbon and water cycles (Bonan, 2008; Laurance et al., 2018; Spracklen et al., 2012), a source of flowers and fruits (de Groot et al., 2002) and their association with fauna will be affected.

Edge effects that arise as a result of the interaction between habitat and non-habitat areas are corollary to forest fragmentation. Due to the peripheral position to which they are exposed, such areas are the first to receive direct and more intense influences from the external anthropic environment. Such influences can be increasing tree mortality, changing tree community composition, reducing canopy cover, increasing the proliferation of pioneer species, declining the population of hardwood trees and reduction of seedling abundance and survival (Laurance et al. 2006a, 2006b; 2000; de Paula et al. 2016; Michalski et al. 2007; Bruna 1999).

Despite the Amazon forest extension, vicissitudes imposed by the main factors of deforestation (e.g. human population density, highways and dry season severity) (Laurance et al. 2002a), make the Amazon forest critically vulnerable to edge effects. Currently, the development of new infrastructure (e.g. hydroelectric dams and roads) would intensify the forest fragmentation (Alamgir et al., 2017; Barona et al., 2010; Fearnside, 2015) , expanding

the areas exposed to edge effect, as occurred in the Brazilian Amazon, that increased the proportion of forest edge from 10% to 25% (Haddad et al., 2015).

Many studies have evaluated the impact of edge effects on tree composition, recruitment, increment, stem density and mortality of Amazon trees (Sizer and Tanner 1999; Mesquita et al. 1999; Laurance, et al. 2006a, 2006b, 2007). However, temporal assessment of the edge effect influences throughout the life of trees become necessary for a better understanding of how individuals of certain species may be affected and react when exposed to altered environments.

In this sense, dendrochronology may be an effective tool for temporal assessing of tree population growth dynamics, reflecting the effect of biotic and abiotic factors on the growth-ring width throughout its life (Babst et al., 2014; Brienen and Zuidema, 2005; Callado et al., 2014; Venegas-González et al., 2018). Moreover, the historical record of growth-rings are able to reveal disturbance events that occurred during the life of the trees (Fraver and White, 2005; Maes et al., 2017), considered discrete episodes in time, that alter the availability of environmental resources and consequently disturb populations, communities and ecosystems (Pickett and White, 1985). The magnitude, timing and duration of those events are usually inferred by growth release (Black et al., 2009), observed in tree-rings as an abrupt increased growth period, sustained over time due to improved light or nutrient condition after mortality of a neighboring tree and a consequent competition reduction (Black et al., 2009; Oliver and Larson, 1996). Such phenomenon may be extended by the new environment and its consequences after the creation of forest edges.

In this study, we used tree-ring lifetime growth patterns, of *Scleronema micranthum* (Ducke) Ducke, Malvaceae, a common tree species (Rankin-de-Mérona et al., 1992), commonly known as “Cardeiro”. The specie is considered a canopy tree, rarely semi-deciduous, presenting annual fructification from September to February and flowering from July to October (Alencar et al., 1979). *Scleronema micranthum* trees exposed and non-exposed to edge effects was selected, in order to address the following questions: (i) Are individual growth patterns of trees located closed to a forest edge affected compared with trees located far from the edges?, (ii) What is the temporal extent of edge effect influence on tree growth patterns?, (iii) Are edge effects boosting release events? We believe that tree-rings are important ecological indicators for revealing the setback or progress condition of forest edge effects, promoting new insights on the resilience ability of trees when exposed to a new scenario of forest fragmentation and its edge effects.

Materials and Methods

Study and sampling areas

The present study was carried out in the Biological Dynamics of Forest Fragments Project (BDFFP) study sites. The BDFFP can be considered the world's largest and longest-running experimental study of habitat fragmentation (Laurance et al., 2018; Lovejoy et al., 1986) which, since 1979, has been evaluating the impacts of forest fragmentation in the Central Amazon forest (Laurance et al. 2002b). Research conducted earlier at the BDFFP has substantially contributed to our understanding of edge effects (Camargo and Kapos 1995; Bruna 1999; Laurance and Yensen 1991; Laurance et al. 1997, 2006a; Uriarte et al. 2010). However, evaluating the temporal influence of edge effects on the tree growth dynamics at BDFFP, from a dendrochronological perspective, has not been studied until now, this study being the pioneer in such approach.

The BDFFP is located 80 km north of Manaus, Amazon, Brazil (2°30'S, 60°W), covering an area of ~1000 km². A description of the project and the location of all fragments and control areas can be found in Gascon and Bierregaard (2001). The annual precipitation ranges from 1900 to 3500 mm with a moderate, but remarkable dry season from June to October (Laurance et al., 2018).

The phytophysiognomy is predominantly forest, characterized by terra firme type of forest, a term designated for non-flooded Amazon forest (Hopkins, 2005), that represent 80% of the Amazon Biome (Pires and Prance, 1985). Four strata define the forest structure (understory, sub-canopy, canopy and emergent), presenting a 25-35 m canopy on average, with emergent trees that can reach up to 45 m, with at least 1300 species (>10cm DBH) (BDFFP personal communication, 2018).

For the present study, two BDFFP reserves were visited to collect wood samples from trunks of *Scleronema micranthum* trees, one of the most abundant and widespread tree species on the study sites (Rankin-de-Mérona et al., 1992). Such abundance allowed us to locate trees exposed and non-exposed to edge effects. Trees exposed to edge effects were located close to the edge or at most, 300 m from any edge in the Porto Alegre farm, specifically at the 100-ha reserve (2°22'2.82"S, 59°58'31.63"W). The reserve was isolated and created in August of 1983, by cutting and burning the surrounding pristine forest to establish new pasture lands. We defined the penetration distance of edge effects up to 300 m because increasing tree mortality associated to forest fragmentation can be detectable until this distance (Laurance et al., 1998). Trees not exposed to edge effects were sampled at Esteio farm, at the continuous forest located within the Km 41 reserve (2°26'15.52"S, 59°46'1.25"W). Trees were located at

least 1000 m from the nearest edge (a narrow unpaved road). The reserve was created in 1984, and the forest was kept intact and used as one of the control areas.

Scleronema micranthum tree-ring analysis

A dendroecological analysis of *Scleronema micranthum* was conducted on 42 adult individuals (≥ 10 cm DBH), 21 potentially exposed to edge effects and 21 not exposed to any edge effects. The sampled trees were in good phytosanitary condition and did not present liana infestation. Three radial cores were collected for each tree at breast height using increment borers (Diameter = 5.1 mm). Each core was polished with different abrasive sand paper (from 80 to 600 grains/cm²) with the aim of revealing growth ring boundaries. Subsequently, all tree-rings were identified with the aid of a stereomicroscope according to the classic method (Stokes and Smiles, 1996), using narrow rings as guides. After identification, all tree-ring series was scanned at a resolution of 2400 dpi by an HP G4050 scanner. Measurement of tree-ring width was performed with precision of 0.001 mm through the software Image J.

To evaluate dating accuracy, the temporal series of ring widths were compared within and among trees at each site. Both visual and statistical cross dating were performed. Visual cross dating was done working with ring-width bar plots, and statistical cross dating was tested using COFECHA software (Holmes, 1983). COFECHA uses segmented temporal series correlation techniques to assess the quality of cross dating and measurement accuracy in the growth ring time series (Grissino-Mayer, 2001).

After evaluating the dating in COFECHA software, we sought to construct master chronologies for each site that would increase the retention of common growth signals. According to Cook and Kairiukstis (1990), spline functions with length between 67% and 75% of the series are able to remove biological growth trends related to high frequency variances. To build site chronologies, time series were detrended and standardized using a smoothed cubic spline function with 50% frequency-response cut-off for 65% of the length of each series in dplR package in R Software (Bunn, 2008). The standardization of the series is performed by dividing the width of the growth ring by the growth model of the smooth cubic spline function, producing dimensionless ring-width indices (RW) (Bunn and Korpela, 2017). The quality of the chronology was evaluated by the value of Rbar and EPS (expressed population signal), both calculated with the dplR package on R Software (Bunn, 2008). The Rbar is the average correlation coefficient resulting from comparing all possible segments of a predetermined length among all the series included in the chronology (Briffa, 1995). The EPS

values provided information that confirmed the existence of common signals among trees, EPS values higher than 0.80 indicate that the limiting factor to growth in the chronology probably is homogenous (Mendivelso et al., 2014).

Site growth patterns

To explore growth patterns among trees located close to the edges and trees located in the interior of the forest, width of the growth rings was converted into basal area increment (BAI). BAI is considered a more informative measure of tree growth trends in terms of total biomass production (Peñuelas et al., 2011; Phipps and Whiton, 1988) and decreasing tendency will only be presented in senescent trees or when trees are subjected to significant growth stress (Duchesne et al., 2003; Jump et al., 2006). The width of the growth ring was converted to BAI according to the following standard formula: $BAI = \pi (R^2n - R^2n-1)$, where R is the tree radius and n is the growth ring formation year. To calculate BAI we used the `bai.out` function in `dplR` package in software R (Bunn and Korpela, 2017; Bunn, 2008).

Principal Component Analysis (PCA) was performed to identify dominant BAI patterns between edge and interior trees during common growth periods: all periods (1941 to 2014), before edge creation (1941 to 1982), five years after edge creation (1983 to 1987), ten years after edge creation (1983 to 1992) and fifteen years after edge creation (1983 to 1997). The PCA was realized by the `prcomp` function in R software (R core Team, 2017). The use of PCA to detect growth patterns is widely employed in dendrochronological studies (Oliveira et al., 2010; Rodríguez-Catón et al., 2016; Venegas-González et al., 2017; Villalba et al., 1998) and by reducing the dimensionality of multivariate data, it supports the results interpretation (Legendre and Legendre, 2012). Through the data dimension reduction, the PCA automatically performs data clustering according to the K-means objective function (Ding and He, 2004). Thus, seeking cluster validation of trees exposed and unexposed to edge effects, Silhouette Index (SI) (Rousseeuw, 1987) was used. The SI evaluates how much a sample is similar to another inserted in the same cluster, comparing with samples inserted in other clusters (Kaufman and Rousseeuw, 2009). SI values near +1 indicate that the sample is far from the neighboring clusters, confirming that the sample was correctly allocated. A value of 0 indicates that the sample is very close to the decision boundary between two neighboring clusters, and negative values indicate that sample might have been assigned to the wrong cluster (Rousseeuw, 1987). After PCA, we used one-way ANOVA with Tukey's post hoc test ($p < 0.05$) to compare BAI trends between edge and interior clusters.

Disturbance analysis

Some of the most widely used methods for identifying release events are radial growth averaging techniques, in which a growth change percentage (%GC) calculation is made on each tree ring time series, and release events are recorded when growth change percent values exceed a certain minimum value (Black et al., 2009; Nowacki and Abrams, 1997). In this way, to detect release events we used the formula of Nowacki and Abrams (1997) to derive the growth change percentages: $\%GC = [(M2 - M1) / M1] \times 100$, where %GC = growth change percentage for year 1, $M1$ = mean diameter growth over the preceding 10 years, and $M2$ = mean diameter growth over the subsequent 10 years. Studies in tropical forests reveal that a moving average of 10 years was able to remove long-term age-effects and short-term climatic fluctuations (R J W Brien et al., 2010; Brien and Zuidema, 2006; Rozendaal et al., 2011). Release events were identified when the %GC was greater than 50% during a minimum period of 10 years (Rozendaal et al., 2011). Release events were performed by overall function by the Nowacki and Abrams (1997) method using the “TRADER” package (Altman et al., 2014) in R (R core Team, 2017).

Seeking to verify if the %GC that promoted release events before and after the edge creation induced statistically significant differences in the wood production, one-way ANOVA with Tukey’s post hoc test ($p < 0.05$) was performed on the growth changes of BAI (Δ BAI). Δ BAI was calculated as the difference in the BAI average ten years before the release events and ten years after the release events. ANOVA was performed by the OAV function in R software (R core Team, 2017).

Results

Tree-rings chronologies of *Scleronema micranthum*

The growth rings of *Scleronema micranthum* trees at both sites were distinct and characterized by tangentially distended rays touching the apotracheal, possibly terminal parenchyma bands (Vetter and Botosso, 1989a) (Figure 1).

The master chronology (Figure 2) was built from tree-ring widths covering 138 years (1878 - 2015) for trees located within the interior of the forest and 142 years (1874 -2015) in trees located close to the edges, confirming the presence of trees all over the forest far before isolation and creation of the reserve in 1983. The cross-dating quality and accuracy in the measurements of the growth rings was confirmed by the correlations, $EPS > 0.80$ and $Rbar > 0.3$ values, indicating a common growth pattern of *Scleronema micranthum* at each site. The descriptive statistics of the chronologies are presented in Table 1.



Figure 1. a) *Scleronema micranthum* tree on edge at Biological Dynamics of Forest Fragments Project site; b) Macro and c) microscopic images of the transverse wood section evidencing the growth ring anatomy characterized by tangentially distended rays touching the apotracheal, possibly terminal parenchyma bands. White triangles indicate the growth-rings limits.

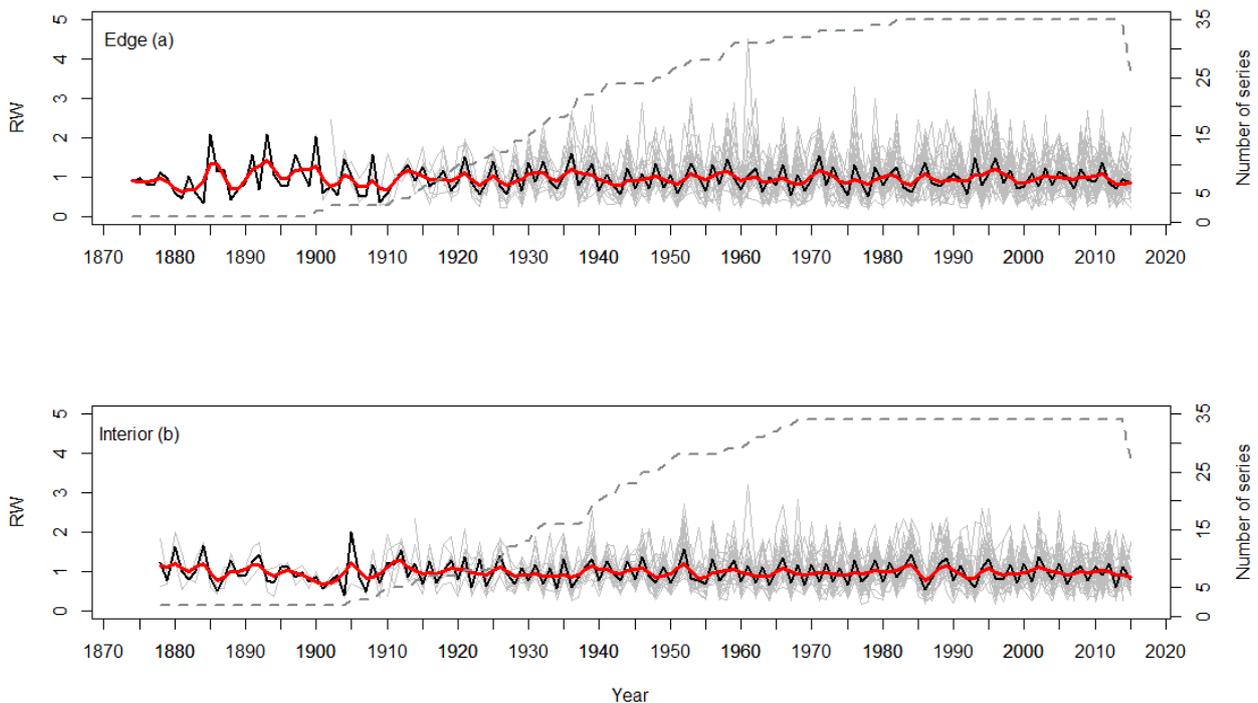


Figure 2. Residual tree-ring chronology of *Scleronema micranthum* trees for Edge (a) and Interior (b) locations in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. Grey solid line: individual average time series; black line: residual tree-ring master chronology; grey dotted line: number of series used for the index calculation; red line: standardization of master chronology by a 10% smoothed spline curve.

Table 1. Descriptive statistics of the chronologies of *Scleronema micranthum* trees located close to the edge and in the interior of the reserve at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.

Variables	Edge	Interior
No. trees/No. radial cores	21/34	21/34
Mean ring width \pm s (cm)	0.18/0.12	0.18/0.09
Time span	1874- 2015	1878-2015
Age \pm s	81/22	81/22
Mean sensitivity	0.56	0.51
Series intercorrelation	0.51	0.50
Rbar (\pm s)	0.4/0.02	0.3/0.05
Period with EPS \geq 0.80	1920-2015	1915-2015

Site growth patterns

After the construction of the chronologies and the growth-ring annuity confirmation, we sought to compare edge and interior population growth patterns with similar age and diameter structure. For this, 15 trees located close to the edge and 15 trees located in the interior of the forest representing age and diameter corresponding population structure of a common growth period (1941 to 2014) were selected (Table 2).

Table 2. Age and diameter at breast height (DBH) of *Scleronema micranthum* trees at edge and interior sites in terra firme forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia selected for growth pattern analyzes.

Year	Edge		Interior	
	DBH	Age	DBH	Age
1941	6.9 (s=5.8)	20 (s=17)	6.9 (s=6.2)	23 (s=18.2)
1982	22.3 (s=6.3)	61 (s=17)	22.1 (s=7.1)	64 (s=19)
2014	33.3 (s=5.2)	92 (s=17.8)	34.9 (s=6.7)	96 (s=12.2)

Principal component analysis (PCA) over a common growth period (1941 to 2014) (Figure 3a) revealed that trees closed to the edge and in the interior of the forest shared basal area increment (BAI), a common sign retained mainly by the Axis 1, responsible for 43% of the data variance and, a more divergent growth signal retained by Axis 2 and responsible for 10% of the variance. The formed clusters presented a weak silhouette coefficient (<0.5), confirming BAI patterns homogeneity throughout the 73 years analyzed.

When performing PCA before forest fragmentation and edge creation (1941 to 1982) (Figure 3b) we observed that the BAI variance retained by component one increases (47%) and the variance retained by component two decreases (9%). Although the variance retained

by Axis 1 and 2 in PCA prior to edge creation are close to the observed in the whole analyzed period (Figure 3a), the non-validation of the cluster by the Silhouette index (<0.2), and the lack of statistically significant differences between BAI series through ANOVA ($F=0.58$, $p=0.44$), confirm that previously forest fragmentation, trees located close to the edge (4.90 cm^2 , $SE = 0.20$) and within the forest interior (4.69 cm^2 ; $SE = 0.17$), presented higher homogeneity in their BAI dynamics.

Although similar BAI patterns are shared (Figure 4), major tendency differences are observed from 1972 to 1990. Before forest fragmentation (1972 to 1982), BAI divergences among trees located close to the edge (4.90 cm^2 ; $SE = 0.51$) and in the forest interior (4.69 cm^2 ; $SE = 0.42$), were not statistically significant according to ANOVA ($F = 0.003$; $p = 0.95$). We can observe in Figure 4 that the divergences occurred before forest fragmentation promoted differences mainly in the BAI amplitude. However, after forest fragmentation, BAI trends were altered, opposing patterns of increase and reduction occurring in wood production within the populations separated by the new environmental conditions promoted by the forest edge. Nonetheless, when we performed the variance analysis ($F = 3.27$, $p = 0.07$) after forest fragmentation (1983 to 2014), edge (15.36 cm^2 ; $SE = 0.6$) and interior trees (14.07 cm^2 ; $SE = 0.4$) still did not present statistically significant differences among BAI series. Thus, we assume that: i) edge effects did not alter the growth dynamics of the trees or ii) edge effects were temporal, reducing the intensity during the 73 years evaluated.

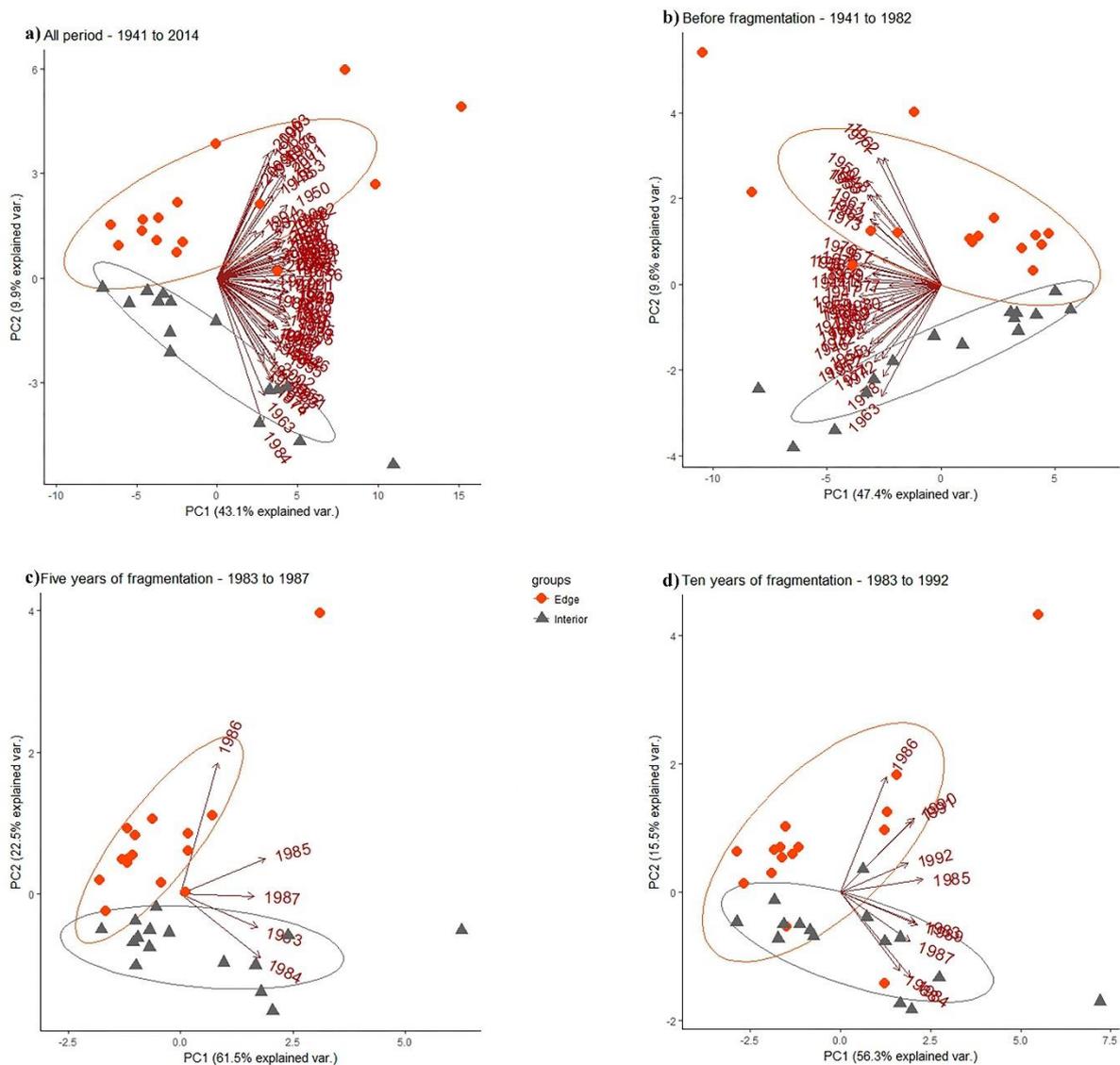


Figure 3. Principal Component Analysis described by BAI series of *Scleronema micranthum* trees located close to the edge (orange circles) and in the interior of the forest (gray triangles) in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.

Our results identified the temporality of edge effects in the growth rings of *Scleronema micranthum* trees mainly in the first 10 years after edge creation. During the first five years (1983 - 1987) ordination analysis showed that the intensity of edge effects was strong enough to cluster edge and interior trees through the second main component, responsible for 22% of the data variance (Figure 3c). Silhouette coefficient > 0.7 supported the ordination. The variance increase retained by component two demonstrates the strength increase of the most divergent BAI signal during the first five years of forest fragmentation and edge creation. In trees located close to the forest edge the result reflected 22% lower wood production during this period, statistically supported by ANOVA ($F = 3.34$, $p = 0.04$). However, the retention of 61% of the data variance by component one still indicates the

sharing of common growth signs between edge and interior trees during the first five years of edge creation.

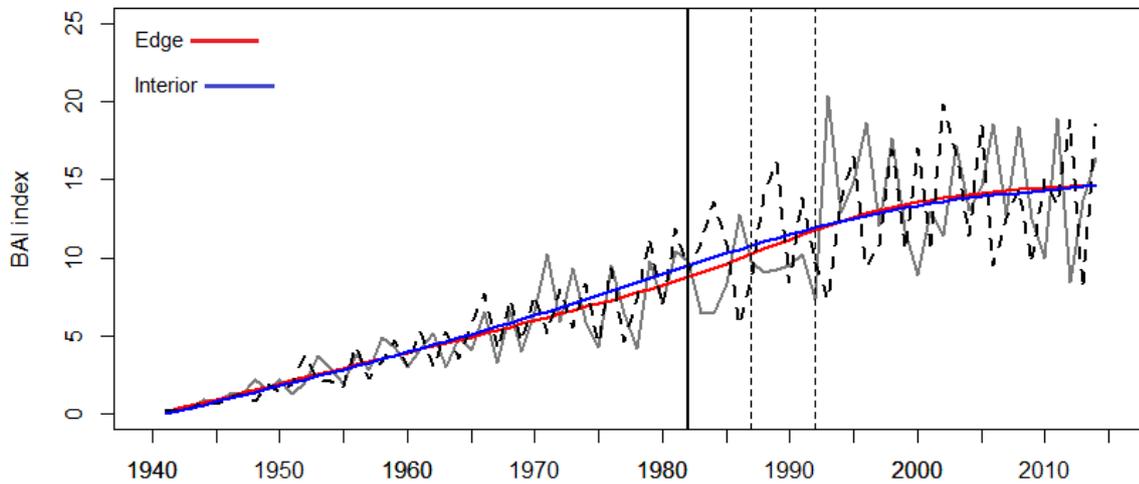


Figure 4. Dominant basal area increment (BAI) index patterns of *Scleronema micranthum* trees located close to the edge (grey solid lines) and in the interior of the forest (black dashed line) in terra firme type of forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. Red line: Standardization by a 30% smoothed spline curve of BAI chronology of trees located close to the edge; blue line: Standardization by a 30% smoothed spline curve of BAI chronology of trees in the interior of the forest; vertical black solid line: edge creation year (1982); vertical black dashed line: five and ten years after edge creation.

When performing the PCA for 10 years after edge creation, we verified that the intensity of the effects that ordered the clusters was reduced to 15% of the variance (Figure 3d), indicating a strength reduction of the most divergent BAI pattern, related to edge effects. Despite the lower strength, the cluster ordination was supported by the silhouette coefficient (= 0.5). The edge effects influenced during the first 10 years resulted in 18% lower wood production (10.4 cm^2 ; SE = 0.58) for trees closed to the edge, compared to those of the interior (12.31 cm^2 ; SE = 0.60), data supported by ANOVA ($F = 5.38$, $p = 0.02$). From the tenth year, BAI differences were not statistically significant by analysis of variance and principal components, presenting non-validated clusters by the Silhouette coefficient <0.4. Table 3 presents the BAI of trees located close to the edge and in the interior of the forest during the analyzed time periods.

Table 3. Basal area increments (BAI) of *Scleronema micranthum* trees located close to the edge (Edge BAI) and in the interior of the forest (Interior BAI) during a common growth time period in *terra firme* forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia. The asterisk indicates the statistically significant differences by one-way ANOVA with Tukey's post hoc test ($p < 0.05$).

	Edge BAI	Interior BAI
All periods - 1941 to 2014	9.42 cm ² , SE=0.32	8.75 cm ² , SE=0.23
Before forest fragmentation - 1941 to 1982	4.90 cm ² , SE = 0.20	4.69 cm ² , SE = 0.17
After forest fragmentation - 1983 to 2014	15.36 cm ² , SE = 0.60	14.07 cm ² , SE = 0.40
Five years of forest fragmentation - 1983 to 1987	*9.62 cm ² , SE=0.71	*11.81 cm ² , SE=0.93
Ten years of forest fragmentation - 1983 to 1992	*10.36 cm ² , SE = 0.58	*12.31 cm ² , SE = 0.60
Fifteen years of forest fragmentation - 1983 to 1997	12.98 cm ² , SE=0.67	12.33 cm ² , SE= 0.49

Disturbance analysis

Disturbance analyses were able to detect differences in growth release events between trees exposed and non-exposed to edge effects (Figure 5). In general, during the evaluated period of 73 years, 47 growth release events were observed in trees located close to the edge, 31 of those events occurred after forest fragmentation and only half of them (16 in total) occurred before the edge creation. About 65% of major events occurred after forest fragmentation and edge creation. Analysis of variance confirmed that the BAI growth changes (Δ BAI) after forest fragmentation (Δ BAI = 7.05 cm²; SE = 1.0) was, on average, 50% higher than those occurred prior to forest fragmentation (Δ BAI = 4.69cm², SE = 0.8). However, ANOVA analyses do not confirm greater differences in the first five and ten years after edge creation.

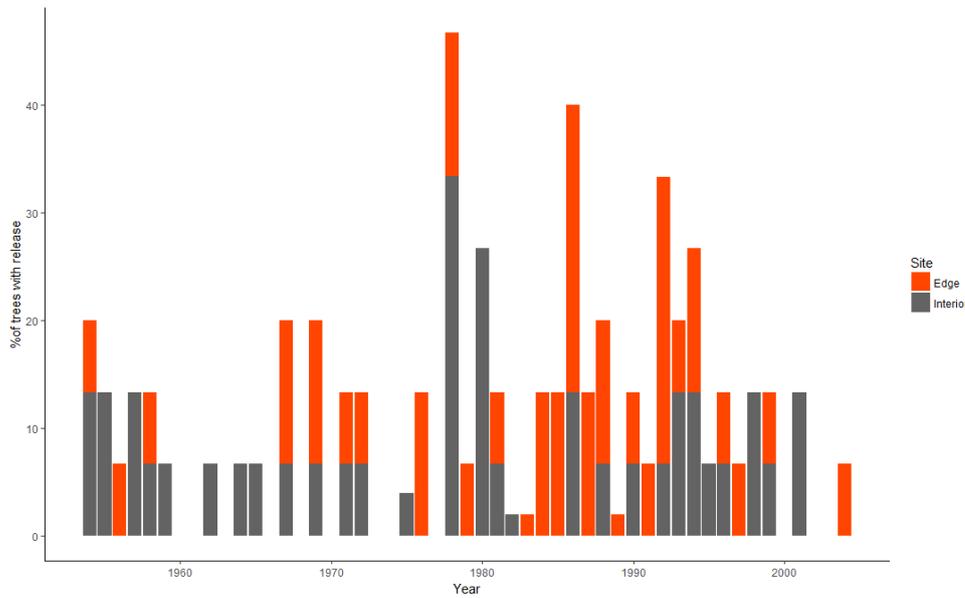


Figure 5. Release events in *Scleronema micranthum* trees close to the forest edge (orange) and in the interior of the forest or far from the edge (gray) in *terra firme* forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.

Trees located close to the edge presented an average diameter at breast height (DBH) of 19 cm ($s=6$) in the years of release events that occurred before edge creation, and 24 cm ($s=5$) DBH in the years of release events that occurred after forest fragmentation. Indicating that in the years of release events, the trees occupied the forest canopy or were close to it.

Trees not exposed to edge effects presented 50 release events over the 73 years evaluated (1941 to 2014). In the release year 56% of the interior trees had an average DBH of 13 cm ($s=3$), indicating a sub-canopy position in the forest vertical profile. This is the opposite of that observed in the previous group of trees that occupied, in most release events, a position in the forest canopy.

Although the number of release events after edge creation is greater in trees close to the edge, they did not result in statistically significant differences in Δ BAI within individuals located close or far from the edge, in the first five, ten and fifteen years after forest fragmentation. Thus, results indicated that disturbances caused by edge effects are inducing an increased number of growth release events in *Scleronema micranthum* trees, but not necessarily increasing Δ BAI compared to the trees located far from the forest edge.

Discussion

Tree-ring chronologies of *Scleronema micranthum* trees

The *Scleronema micranthum* dendrochronological potential has been recognized since the pioneering works of Vetter and Botosso (1989a; 1989b; 1988) which confirmed, through anatomical structures, climatic relationships and incision in the vascular cambium (Mariaux window), the growth ring annual formation. The high value of correlation, EPS and Rbar reached by the edge and interior chronologies, is strong evidence that the growth rings are indeed synchronized with the annual calendar, proving the existence of a common sign among trees (Briffa, 1995; Stahle, 1999).

The annual dry season present in the region from July to September with a monthly precipitation near 60 mm should be a growth limiting factor (Stokes and Smiles, 1996) capable of inducing a seasonal rhythm of wood formation (Worbes, 1995), and therefore the existence of annual growth rings in *Scleronema micranthum* trees.

Site growth patterns

Growth rings demonstrated to be quite valuable archives of the annual variability of tree growth (Babst et al., 2014; Brienen et al., 2016), providing, through an annual dimension, a great refinement in studies of forest dynamics (Biondi, 1999) and specifically, as focused on in our study, a refinement in studies on edge effects after forest fragmentation. Mainly through PCA and ANOVA results there was indication of the return of a common growth pattern between trees located close to the forest edge and within in the interior of the forest only after 10 years of forest fragmentation. This revealed that edge areas, besides losing significant amounts of biomass via mortality of large trees during the first five years of forest fragmentation (Laurance et al., 2007), can continue to affect the basal area increment dynamics of the surviving trees for at least another 10 years. According to Stephenson et al (2014), old survival trees do not act simply as senescent carbon reservoirs, but actively fix large amounts of carbon compared to smaller trees. Thus, the BAI reduction of surviving trees during the first 10 years of edge creation, probably can also reduce the carbon stock potential of old trees in fragmented areas.

After forest fragmentation, the carbon reservoir role is redistributed within the trees and in the first years of restoration is mainly associated with the growth of early-successional species. During the last stages of succession, the slow growing trees will contribute more significantly (Shimamoto et al., 2014). This result reflects the increased tree mortality (Laurance et al., 2006a, 1998) and elevated photo-synthetically active radiation (PAR) caused

by lateral light penetration from the nearby clearing (Sizer and Tanner 1999) that favored an increase in the diameter increment in early-successional species (0 to 50 cm DBH) (McDonald and Urban 2004). Surveys in BDFFP study sites proved that faster-growing species have increased density and basal area increments in the forest edge, favored mainly by the stand-level tree mortality and the number of nearby forest edges, shifts that can become even more abundant over time (Laurance, et al. 2006b). Simultaneously, many slow-growth tree species are disfavored by the new environmental condition, and eventually may be driven to local extinction (Michalski et al., 2007). In undisturbed forests at the BDFFP, Laurance et al (2004) revealed, for a period of 15 years, a tendency for canopy and emergent trees to increase in population density and basal area compared to small trees and justifies that the most likely cause of higher productivity in undisturbed Amazon forest is because of rising atmospheric CO₂ levels.

However, for disturbed Amazon forest, our dendrochronology approach revealed that the consequences can be distinct. We identified, that late-succession trees, such as *Scleronema micranthum* (Marengo and Vieira, 2005), when remaining in edge areas after forest fragmentation, can present a lowest basal area increment in the first 10-year period. In other words, edge effects may reduce canopy tree productivity for a least 10 years. In reserves of 1 ha (highest forest/edge ratio) at the BDFFP, *Scleronema micranthum* trees fructify outside the period normally expected for the species (September to February) and reduce the flowering period, indicating a probable disturbance in the flower and fruit production process in fragmented areas (Rankin de Merona and Ackerly, 1987), results associated to reduced productivity that can alter their ecosystem services.

By occupying a canopy position in the year of edge creation, *Scleronema micranthum* tree crowns are exposed to intense sunlight and evapotranspiration. Thus, knowing that large tropical trees are vulnerable to droughts (Condit et al., 1995), this late-succession tree species can be more sensitive to a desiccation increase (Kapos, 1989) in edge areas. As such, it is believed that the micro-climatic changes, such as elevated temperatures, reduced humidity and increased vapor pressure deficits, occurring in newly created edges lead to depleted soil moisture, creating drought stress (Camargo and Kapos, 1995; Malcolm, 1998; Pinto et al., 2010; Sizer and Tanner, 1999). This situation may have influenced the lower wood production in *Scleronema micranthum* trees mainly after the first ten years of edge creation. These are results which, added to the expected temperature increase due to climate change (Allen et al., 2015), can have important consequences for trees exposed to the edge effects.

The resumption of the more homogeneous BAI pattern after 10 years reflects the edge

evolution phases, which after five years of forest fragmentation, presented greater stability in the edge-related changes favored by the progressive growth of secondary vegetation that seals the edge (Camargo and Kapos, 1995; Harper et al., 2005). Although edge effects can be considered one of the main drivers of ecological change in the BDFFP fragments, at least over the first 3 - 4 decades after edge creation (Laurance et al., 2018), the dendrochronological approach identified major influences on the *Scleronema micranthum* tree BAIs during the first 10 years of forest fragmentation and edge creation. Thus, we can consider the secondary forest that regenerated after forest fragmentation as a facilitator of the resumption of the common growth pattern for the *Scleronema micranthum* trees exposed to edge effects, corroborating with the classical ecological theory of Clements; that of a superorganism that recovers and adjusts after undergoing some sort of impact. In this way, we highlight the importance and necessity of preservation of secondary forests after forest fragmentation processes for the maintenance of impacted areas, as areas under edge effects.

Disturbance analysis

A release event is identified in the growth rings as a period of sudden increase in growth over time (Nowacki and Abrams, 1997). These events can be associated with increases in light or water availability following a disturbance that removes or reduces surrounding competitors (Black et al., 2009; Brienen and Zuidema, 2006; White and Pickett, 1985). Edge areas are recognized by increased light incidence (Camargo and Kapos, 1995; Lovejoy et al., 1986; Williams-Linera, 1990) and tree mortality (Laurance et al., 2000; McDowell et al., 2018; Mesquita et al., 1999), favoring release events in trees close to forest edge after edge creation.

By identifying that trees exposed to edge effects exhibit a greater number of release events, disturbance analyzes admit that edge effects induce tree growth increase (Harper et al., 2005). This result appears to be opposite to that observed in the analysis of growth patterns that proved, during the first 10 years of forest fragmentation (1983 to 1992), a lower BAI in trees located close to edges compared to the trees in the interior of the forest. However, when we analyzed only the trees located close to the edge we observed that release events after forest fragmentation really induced 50% greater Δ BAI in relation to events prior to edge creation. That is, release events after forest fragmentation promoted higher growth changes in edge trees than those that occurred prior to fragmentation, although this difference does not reflect higher growth in relation to interior trees.

The vertical light gradient created by the forest canopy represents the greatest challenge for tree establishment, particularly canopy trees (Harcombe and Marks, 1978). Consequently, in order to reach the forest canopy, saplings of many species require periods of increased light (areas close to gaps) (Brokaw, 1985; Yamamoto, 2000). Hence, trees that do not occupy a canopy position are expected to exhibit larger release events (R J W Brienen et al., 2010; Rozendaal et al., 2011). However, our study revealed that release events in edge areas that promoted higher Δ BAI were performed by *Scleronema micranthum* canopy trees after forest fragmentation. This could indicate release advantages in canopy trees that survived to edge creation, increasing the competition for sunlight capture, what could harm the canopy ascension in trees of lower strata, changing the forest dynamics. However, when surviving trees are infested by lianas, the leaf shading of the phorophyte may reduce the growth rates and the number of release events in trees exposed to edge effects, as observed in *Aspidosperma polyneuron* trees in the Brazilian Atlantic Rain Forest (Godoy-Veiga et al., 2018). These results are not observed in our study due to the absence of liana infestation in *Scleronema micranthum* trees, evidencing more strongly the edge effect as an important (and temporary) factor of systemic imbalance.

Through the disturbance analysis, we identify the hyperdynamic tendencies in fragmented areas (Laurance, 2002; Laurance et al., 2018), reflecting the release event frequency increase and Δ BAI amplitude increase after edge creation. The hyperdynamism in fragmented areas can have serious ecological impacts, altering disturbance regimes, mortality and recruitment and turnover rates, population fluctuations of individual species, species local extinction, and the pace of biogeochemical cycling (Laurance, 2002). However, the return to the more homogeneous BAI pattern between edge and interior location and the presence of only six release events in trees located close to the forest edge after 10 years of fragmentation may indicate that the hyperdynamic tendency of *Scleronema micranthum* growth may gradually stabilize and approach the pre-fragmentation condition after 10 years of edge creation. However, considering that fragmented areas are more susceptible to stochastic events (de Paula et al., 2016), the temporality of the hyperdynamic condition may be extended even longer.

Conclusions

Through the growth-ring analysis we revealed that the edge effects on *terra firme* type of forest in Central Amazon are changing the growth dynamics of the *Scleronema micranthum* trees for at least 10 years after edge creation, inducing an 18% reduction in tree

growth in this period. The resumption of the more homogeneous BAI pattern between trees located at the edge and in the interior of the forest after 10 year of edge creation proves the temporal extension of edge effects, presenting greater stability in the edge-related changes favored by the growth of secondary vegetation that progressively seals the edge or at least diminishes its effects. The increase in release events after edge creation reflects the hyperdynamic condition of fragmented areas, although this result does not manifest itself in greater growth in relation to trees not exposed to edge effects. This study demonstrates the potential of tree ring analysis in evaluating the temporal extent of edge effects, promoting a future perspective of management and forest conservation. We therefore emphasize the potential and importance of considering growth-rings as relevant ecological indicators of historical environmental changes associated with forest fragmentation.

Acknowledgements

This work was funded by the Rufford Small Grant for Nature Conservation (<http://www.rufford.org/>, RSGA application 18762-1), BDFFP Thomas Lovejoy research fellowship program and conducted during a scholarship supported by the International Cooperation Program CAPES/PVE (process: 88887.127558/2016-00) at Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Mendoza, Argentina. The first author was supported by a PhD scholarship from CAPES – Brazilian Federal Agency for the Improvement of Higher Education Personnel. This is the number 750 publication of the Biological Dynamics of Forest Fragment Project (BDFFP – INPA/STRI) Technical Series.

References

- Alamgir, M., Campbell, M.J., Sloan, S., Goosem, M., Clements, G.R., Mahmoud, M.I., Laurance, W.F., 2017. Economic, socio-political and environmental risks of road development in the Tropics. *Curr. Biol.* 27, 1130–1140.
- Alencar, J. da C., de Almeida, R.A., Fernandes, N.P., 1979. Fenologia de espécies florestais em floresta tropical úmida de terra firme na Amazônia Central. *Acta Amaz.* 9, 163-198.
- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, 1–55.
- Altman, J., Fibich, P., Dolezal, J., Aakala, T., 2014. TRADER: a package for tree ring analysis of disturbance events in R. *Dendrochronologia* 32, 107–112.

- Babst, F., Alexander, M.R., Szejner, P., Bouriaud, O., Klesse, S., Roden, J., Ciais, P., Poulter, B., Frank, D., Moore, D.J.P., 2014. A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* 176, 307–322.
- Barona, E., Ramankutty, N., Hyman, G., Coomes, O.T., 2010. The role of pasture and soybean in deforestation of the Brazilian Amazon. *Environ. Res. Lett.* 5, 24002-24011.
- Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecol. Appl.* 9, 216–227.
- Black, B.A., Abrams, M.D., Rentch, J.S., Gould, P.J., 2009. Properties of boundary-line release criteria in North American tree species. *Ann. For. Sci.* 66, 205-206.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449.
- Brienen, R.J.W., Schöngart, J., Zuidema, P.A., 2016. Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees, in: *Tropical Tree Physiology*. Springer, pp. 439–461.
- Brienen, R.J.W., Zuidema, P.A., 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *J. Ecol.* 94, 481–493.
- Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146, 1–12.
- Brienen, R.J.W., Zuidema, P.A., Martinez-Ramos, M., 2010. Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions. *Oecologia* 163, 485–496.
- Briffa, K.R., 1995. Interpreting high-resolution proxy climate data—the example of dendroclimatology, in: *Analysis of Climate Variability*. Springer, pp. 77–94.
- Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66, 682–687.
- Bruna, E.M., 1999. Biodiversity: seed germination in rainforest fragments. *Nature* 402, 139-140.
- Bunn, A., Korpela, M., 2017. An introduction to dplR.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124.
- Callado, C.H., Vasconcellos, T.J., Costa, M.S., Barros, C.F., Roig, F.A., Tomazello-Filho, M., 2014. Studies on cambial activity: advances and challenges in the knowledge of growth dynamics of Brazilian woody species. *An. Acad. Bras. Cienc.* 86, 277–284.
- Camargo, J.L.C., Kapos, V., 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* 11, 205–221.

- Condit, R., Hubbell, S.P., Foster, R.B., 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.* 65, 419–439.
- Cook, E.R., Kairiukstis, L.A., 1990. *Methods of dendrochronology: applications in the environmental sciences.* Kluwer, Amsterdam.
- de Groot, R.S., Wilson, M.A., Boumans, R.M.J., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecol. Econ.* 41, 393–408.
- de Paula, M.D., Groeneveld, J., Huth, A., 2016. The extent of edge effects in fragmented landscapes: Insights from satellite measurements of tree cover. *Ecol. Indic.* 69, 196–204.
- Ding, C., He, X., 2004. K-means clustering via principal component analysis, in: *Proceedings of the Twenty-First International Conference on Machine Learning.* ACM, p. 29.
- Duchesne, L., Ouimet, R., Morneau, C., 2003. Assessment of sugar maple health based on basal area growth pattern. *Can. J. For. Res.* 33, 2074–2080.
- Fearnside, P.M., 2015. Hidrelétricas na Amazônia: impactos ambientais e sociais na tomada de decisões sobre grandes obras. *Manaus Ed. do INPA* 1, 296.
- Fraver, S., White, A.S., 2005. Identifying growth releases in dendrochronological studies of forest disturbance. *Can. J. For. Res.* 35, 1648–1656.
- Gascon, C., Bierregaard Jr, R.O., 2001. The biological dynamics of forest fragments project. *Lessons from Amaz. Ecol. Conserv. a Fragm. For.* 31–42.
- Godoy-Veiga, M., Ceccantini, G., Pitsch, P., Krottenthaler, S., Anhuf, D., Locosselli, G.M., 2018. Shadows of the edge effects for tropical emergent trees: the impact of lianas on the growth of *Aspidosperma polyneuron*. *Trees* 32, 1073–1082.
- Grissino-Mayer, H.D., 2001. Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. *Tree-Ring Res.* 57, 205–221.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, 1-9.
- Harcombe, P.A., Marks, P.L., 1978. Tree diameter distributions and replacement processes in southeast Texas forests. *For. Sci.* 24, 153–166.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D.A.R., Jaiteh, M.S., Esseen, P., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conserv. Biol.* 19, 768–782.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43, 69–78.

- Hopkins, M.J.G., 2005. Flora da Reserva Ducke, Amazonas, Brasil. *Rodriguésia* 9–25.
- Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Chang. Biol.* 12, 2163–2174.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185.
- Kaufman, L., Rousseeuw, P.J., 2009. Finding groups in data: an introduction to cluster analysis. John Wiley & Sons.
- Laurance, W.F., 2002. Hyperdynamism in fragmented habitats. *J. Veg. Sci.* 13, 595–602.
- Laurance, W.F., Albernaz, A.K.M., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M., Da Costa, C., 2002a. Predictors of deforestation in the Brazilian Amazon. *J. Biogeogr.* 29, 737–748.
- Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., Meyer, C.F.J., Bobrowiec, P.E.D., Laurance, S.G.W., 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biol. Rev.* 93, 223–247.
- Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Conservation: rainforest fragmentation kills big trees. *Nature* 404, 836.
- Laurance, W.F., Ferreira, L. V, Rankin-de Merona, J.M., Laurance, S.G., 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79, 2032–2040.
- Laurance, W.F., Laurance, S.G., Ferreira, L. V, Rankin-de Merona, J.M., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. *Science* 278, 1117–1118.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002b. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.* 16, 605–618.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizao, R.C.C., Ribeiro, J.E., 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS One* 2, 1017-2007.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J., Harms, K.E., 2006a. Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Natl. Acad. Sci.* 103, 19010–19014.

- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., Capretz, R.L., 2006b. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87, 469–482.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C., Lovejoy, T.E., Andrade, A., D'angelo, S., Ribeiro, J.E., 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428, 171.
- Laurance, W.F., Yensen, E., 1991. Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv.* 55, 77–92.
- Legendre, P., Legendre, L.F.J., 2012. *Numerical ecology*. Elsevier.
- Lovejoy, T.E., Bierregaard Jr, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown Jr, K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., 1986. Edge and other effects of isolation on Amazon forest fragments.
- Lovejoy, T.E., Nobre, C., 2018. Amazon Tipping Point. *Science Advances* 4, 2340-2342.
- Maes, S.L., Vannoppen, A., Altman, J., Van den Bulcke, J., Decocq, G., De Mil, T., Depauw, L., Landuyt, D., Perring, M.P., Van Acker, J., 2017. Evaluating the robustness of three ring-width measurement methods for growth release reconstruction. *Dendrochronologia* 46, 67–76.
- Malcolm, J.R., 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Clim. Change* 39, 487–502.
- Marengo, R.A., Vieira, G., 2005. Specific leaf area and photosynthetic parameters of tree species in the forest understorey as a function of the microsite light environment in central Amazonia. *J. Trop. For. Sci.* 17, 265–278.
- MCDonald, R.I., Urban, D.L., 2004. Forest edges and tree growth rates in the North Carolina Piedmont. *Ecology* 85, 2258–2266.
- McDowell, N., Allen, C.D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., 2018. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol.* 219, 851-869.
- Mendivelso, H.A., Camarero, J.J., Gutiérrez, E., Zuidema, P.A., 2014. Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity. *Agric. For. Meteorol.* 188, 13–23.
- Mesquita, R.C.G., Delamônica, P., Laurance, W.F., 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol. Conserv.* 91, 129–134.
- Michalski, F., Nishi, I., Peres, C.A., 2007. Disturbance-Mediated Drift in Tree Functional Groups in Amazonian Forest Fragments. *Biotropica* 39, 691–701.

- Millenium Ecosystem Assessment, 2003. Ecosystems and human well-being: a framework for assessment. Island Press, Washington, DC, USA.
- Nowacki, G.J., Abrams, M.D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* 67, 225–249.
- Oliveira, J.M., Roig, F.A., Pillar, V.D., 2010. Climatic signals in tree-rings of *Araucaria angustifolia* in the southern Brazilian highlands. *Austral Ecol.* 35, 134–147.
- Oliver, C.D., Larson, B.C., 1996. Forest stand dynamics: updated edition. John Wiley and sons.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., 2011. A large and persistent carbon sink in the world's forests. *Science.* 333, 988–993.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* 20, 597–608.
- Phipps, R.L., Whiton, J.C., 1988. Decline in long-term growth trends of white oak. *Can. J. For. Res.* 18, 24–32.
- Pickett, S.T.A., White, P.S., 1985. The ecology of natural disturbance and patch dynamics, The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.
- Pinto, S.R.R., Mendes, G., Santos, A.M.M., Dantas, M., Tabarelli, M., Melo, F.P.L., 2010. Landscape attributes drive complex spatial microclimate configuration of Brazilian Atlantic forest fragments. *Trop. Conserv. Sci.* 3, 389–402.
- Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon.
- R core Team, R., 2017. R language definition. Vienna, Austria R Found. Stat. Comput.
- Rankin-de-Mérona, J.M., Prance, G.T., Hutchings, R.W., Silva, M.F. da, Rodrigues, W.A., Uehling, M.E., 1992. Preliminary results of a large-scale tree inventory of upland rain forest in the Central Amazon. *Acta Amaz.* 22, 493–534.
- Rankin de merona, J.M., Ackerly, D.D., 1987. Estudos populacionais de árvores em florestas fragmentadas e as implicações para conservação in situ das mesmas na floresta tropical da Amazônia Central. *Rev. IPEF* 35, 47–59.
- Rodríguez-Catón, M., Villalba, R., Morales, M., Srur, A., 2016. Influence of droughts on *Nothofagus pumilio* forest decline across northern Patagonia, Argentina. *Ecosphere* 7, 1390-1407.
- Rousseeuw, P.J., 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *J. Comput. Appl. Math.* 20, 53–65.

- Rozendaal, D.M.A., Soliz-Gamboa, C.C., Zuidema, P.A., 2011. Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis. *Trees* 25, 115–124.
- Shimamoto, C.Y., Botosso, P.C., Marques, M.C.M., 2014. How much carbon is sequestered during the restoration of tropical forests? Estimates from tree species in the Brazilian Atlantic forest. *For. Ecol. Manage.* 329, 1–9.
- Sizer, N., Tanner, E.V.J., 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biol. Conserv.* 91, 135–142.
- Spracklen, D. V, Arnold, S.R., Taylor, C.M., 2012. Observations of increased tropical rainfall preceded by air passage over forests. *Nature* 489, 282.
- Stahle, D.W., 1999. Useful strategies for the development of tropical tree-ring chronologies. *Iawa J.* 20, 249–253.
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90.
- Stokes, M.A., Smiles, T., 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.
- Uriarte, M., Bruna, E.M., Rubim, P., ANCIaes, M., Jonckheere, I., 2010. Effects of forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site limitation. *Ecology* 91, 1317–1328.
- Venegas-González, A., Brancalion, P.H.S., Albiero, A., Chagas, M.P., Anholetto, C.R., Chaix, G., Tomazello Filho, M., 2017. What tree rings can tell us about the competition between trees and lianas? A case study based on growth, anatomy, density, and carbon accumulation. *Dendrochronologia* 42, 1–11.
- Venegas-González, A., Roig, F.A., Lisi, C.S., Albiero-Junior, A., Alvares, C.A., Tomazello-Filho, M., 2018. Drought and climate change incidence on hotspot Cedrela forests from the Mata Atlântica biome in southeastern Brazil. *Glob. Ecol. Conserv.* 15, 408-420.
- Vetter, R.E., Botosso, P.C., 1989a. Remarks on age and growth-rate determination of amazonian trees. *Iawa Bull.* 10, 133–145.
- Vetter, R.E., Botosso, P.C., 1989b. El Niño may affect growth behaviour of Amazonian trees. *GeoJournal* 19, 419–421.
- Vetter, R.E., Botosso, P.C., 1988. Observações preliminares sobre a periodicidade e taxa de crescimento em árvores tropicais. *Acta Amaz.* 18, 189–196.

- Villalba, R., Grau, H.R., Boninsegna, J.A., Jacoby, G.C., Ripalta, A., 1998. Tree-ring evidence for long-term precipitation changes in subtropical South America. *Int. J. Climatol.* 18, 1463–1478.
- Wesselingh, F.P., Hoorn, C., Kroonenberg, S.B., Antonelli, A., Lundberg, J.G., Vonhof, H.B., Hooghiemstra, H., 2010. On the origin of Amazonian landscapes and biodiversity: a synthesis. *Amaz. Landsc. Species Evol. A look into past* 419–431.
- White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: An introduction. *Unkn. J.* 3–13.
- Williams-Linera, G., 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78, 356–373.
- Worbes, M., 1995. How to measure growth dynamics in tropical trees - A review. *Iawa J.* 16, 337–351.
- Yamamoto, S.-I., 2000. Forest gap dynamics and tree regeneration. *J. For. Res.* 5, 223–229.

Chapter 2

AMAZONIAN TREES SHOW INCREASED EDGE EFFECTS DUE TO ATLANTIC OCEAN WARMING AND NORTHWARD DISPLACEMENT OF THE INTERTROPICAL CONVERGENCE ZONE SINCE 1980

Published in the journal: Science of the Total Environment, v. 693, n. 133515

Alci Albiero-Júnior^a; José Luís Campana Camargo^b; Fidel Alejandro Roig^{a,c,d,g}; Jochen Schöngart^e; Renan Mercuri Pinto^f; Alejandro Venegas-González^g; Mario Tomazello-Filho^a

^aUniversity of São Paulo, Luiz de Queiroz College of Agriculture, Department of forest Sciences, Wood Anatomy and Tree-Ring Laboratory, Av. Pádua Dias 11, P.O. Box 9, 13418-900 Piracicaba, SP, Brazil

^bBiological Dynamics of Forest Fragments Project (BDFFP), Manaus, AM, Brazil

^cLaboratorio de Dendrocronología e Historia Ambiental, IANIGLA, CCT CONICET Mendoza, CC 330, M5502IRA, Argentina

^dFacultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Almirante Brown 500, Mendoza Argentina

^eNational Institute of Amazonian Research, Av. André Araújo, 2936 Petrópolis, Manaus, AM, Brazil 69067-375, Brazil

^fSão Paulo State Technological College - CEETEPS, Faculty of Technology of Americana - FATEC, Americana, SP, Brazil

^gHémera Centro de Observación de la Tierra, Escuela de Ingeniería Forestal, Facultad de Ciencias, Universidad Mayor, Santiago 8340589, Chile

* Corresponding author: albierojunior@usp.br

Abstract

Recent investigations indicate a warming of Atlantic Ocean surface waters since 1980, probably influenced by anthropic actions, inducing rainfall intensification mainly during the rainy season and slight reductions during the dry season in the Amazon. Under these climate changes, trees in upland forests (*terra firme*) could benefit from the intensification of the hydrological cycle and could also be affected by the reduction of precipitation during the dry season. Results of dendrochronological analyses, spatial correlations and structural equation models, showed that *Scleronema micranthum* (Ducke) Ducke (Malvaceae) trees exposed in fragmented areas and to edge effects in Central Amazonian *terra firme* forest were more sensitive to the increase in the Atlantic Ocean surface temperature and consequent northward

displacement of the Intertropical Convergence Zone, mainly during the dry season. Therefore, we proved that in altered and potentially more stressful environments such as edges of fragmented forests, recent anthropogenic climatic changes are exerting pressure on tree growth dynamics, inducing alterations in their performance and, consequently, in essential processes related to ecosystem services. Changes that could affect human well-being, highlighting the need for strategies that reduce edge areas expansion in Amazon forests and anthropic climate changes of the Anthropocene.

Keywords: Tree rings; Dendroclimatology; Climate changes, Forest fragmentation; Atlantic Ocean; Biological Dynamics of Forest Fragments Project

Introduction

Contemporary environmental problems, marked by forest fragmentation, biodiversity loss, global warming and growth of social inequality, are Anthropocene marks (Crutzen and Stoermer, 2000), a geological age where human beings begin to destroy essential processes to our own human well-being in an unprecedented way (Roosevelt, 2013).

In this sense, the Amazon Basin plays a fundamental role globally in the maintenance and conservation of processes essential to human well-being, which can be recognized through ecosystem services, depending on how people value nature (Fearnside, 1997; Thompson and Barton, 1994). The Amazon comprises the world's largest continuous rainforest within the largest watershed on earth (Wesselingh et al., 2010), and is considered the richest assembly of plants on the planet, encompassing an estimated (16,000) tree species (Ter Steege et al., 2013b). It is indispensable for the maintenance of ecosystem services and the global carbon cycle (Malhi et al., 2006; Saatchi et al., 2007) through photosynthetic fixation of 17% of the terrestrial carbon biomass (Fauset et al., 2015). It also contributes with ~17% of total global freshwater input to the oceans (Callede et al., 2010) and to the energy balance and climate maintenance of the planet (Hilker et al., 2014; Wang and Fu, 2007).

Research using isotopic analyses of precipitation revealed that 75% of the rainfall in the Amazon Basin originates from the Atlantic Ocean by trade winds and 25% is recycled from the forest surface (Angelini et al., 2011). This large-scale atmospheric circulation pattern is influenced by the establishment of a South American Monsoon System (SAMS). This system is controlled by large-scale ocean thermodynamic conditions near the equatorial zone that promote strong precipitation seasonality and a relatively rapid transition between wet and dry seasons associated with the beginning of the rainy season (Nobre et al., 2009b). In addition, the contribution of the forest to the dynamics of the hydrological regime is explained by water vapor released into the atmosphere by evapotranspiration, which represents energy available to accelerate the air and propel the winds favoring the rains (Makarieva et al., 2013).

According to Marengo and Espinoza (2016), precipitation over the Amazon Basin can be altered by changes in land cover and forest fragmentation, reducing forest evapotranspiration rates and affecting downwind rainfall and hence, the water cycle (Marengo, 2006; Zemp et al., 2014). This enhances the extreme episodes of drought (1995, 1998, 2005, 2007 and 2010) (Gloor et al., 2013, 2015), and flood (2008 - 2009, 2011 - 2012 and 2013 - 2014) (Gloor et al., 2013, 2015), observed during the last three decades in the Amazon, associated mainly with Atlantic and Pacific Ocean surface temperature changes (Barichivich et al., 2018; Marengo et al., 2008; Zeng et al., 2008). Consequently, these extreme drought and flood events may have promoted high tree mortality rates, substantially contributing to atmospheric carbon release and potentiating greenhouse and climate change effects (Phillips et al., 2009). Therefore, identification of how tree species in the world's largest hydrographic basin are affected and respond to climate change is indispensable to understanding how the Anthropocene climatic variability and forest fragmentation projections may modify Amazon forest dynamics and resilience.

By adding a long-term perspective, dendrochronology is an effective tool to evaluate how climate influences tropical tree growth dynamics throughout their life spans (Fontana et al., 2018; Granato-Souza et al., 2018; Venegas-González et al., 2018). Thus, consider that (i) tropical tree growth dynamics is mainly associated with precipitation fluctuations (Brienen et al., 2016; Worbes, 1995), and (ii) that rainfall variability over the Amazon Basin is strongly related to variations in sea surface temperatures of the Atlantic Ocean (A.SST) and the Pacific Ocean (P.SST) (Yoon and Zeng, 2010). In this study we evaluate the sensitivity of tree rings to local and large-scale climate variability in a region of Central Amazonia. We use tree-ring lifetime growth pattern information, using the widespread tree known commonly in Portuguese as *cardeiro*, *Scleronema micranthum* (Ducke) Ducke, Malvaceae (Rankin-de-Merona et al., 1992), as a bioindicator of the reaction of exposed and non-exposed forest to edge effects. We hypothesized that growth-rings of trees from fragmented and edge areas were more sensitive to precipitation, and hence to ocean surface temperature increases, mainly during the last three decades. This is sustained by the influence of microclimate changes in edge areas, that induce drought stress due to temperature increases, humidity decreases, increases of vapor pressure deficit and depletion of soil moisture (Camargo & Kapos, 1995; Malcolm, 1998; Sizer & Tanner, 1999; Pinto et al., 2010).

Materials and Methods

Study and sampling areas

The present study was carried out in the Biological Dynamics of Forest Fragments Project (BDFFP). The BDFFP is located 80 km north of Manaus, Central Amazonia, Brazil (2°30'S, 60°W), covering an area of ~1000 km². A description of the project and the location of all fragments and control areas can be found in Gascon and Bierregaard (2001). Annual precipitation ranges from 1,900 to 3,500 mm with a moderate, but distinct dry season from June to October (Laurance et al., 2018). Figure 6 represents the climatic diagram of monthly averages of minimum, mean and maximum temperatures and precipitation in the study area based on historical data (1941 to 2014) obtained from the Climatic Research Unit (CRU) TS 4.02 and with a grid resolution of 0.5° (Harris et al., 2014).

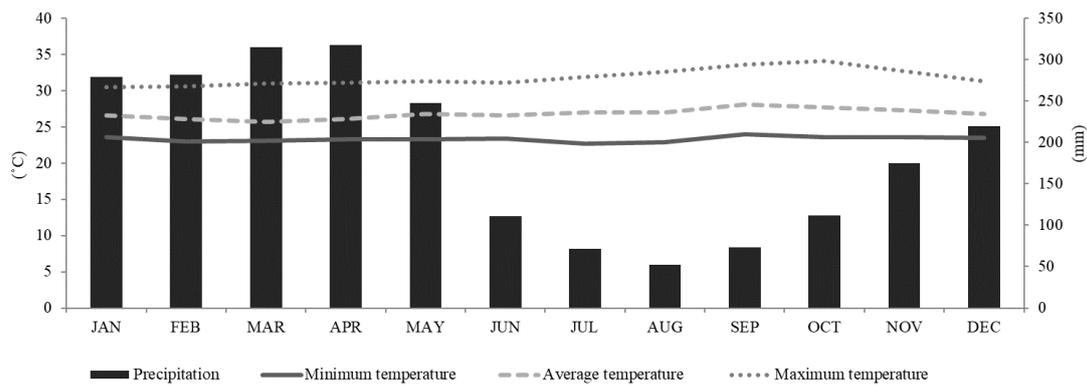


Figure 6. Minimum, mean and maximum temperatures (continuous line, dashed line and dotted line, respectively) and mean monthly precipitation (bars) in Central Amazonia from 1941 to 2014, based on Climatic Research Unit (CRU) TS4.02 0.5° gridded data set (Harris *et al.* 2014).

Under a phytophysiology-based definition, the sampled area is typified as a closed forest of *terra firme*, a term used for non-flooded Amazon forest, which represents 80% of the Amazon Biome (Pires and Prance, 1985). At least, 1,300 tree species (>10 cm DBH) have been recorded so far in these forests (BDFFP personal communication, 2019). Forest vertical structure may be classified into four: understory, sub-canopy, canopy and emergent trees, where the canopy presents a range of height from 25 – 35 m, and emergent trees may reach to 45 m. Crowns of adult *Scleronema micranthum* trees are one of the canopy components and even taller individuals occasionally may be found being one of the most abundant and widespread species in the selected study sites (Rankin-de-Merona et al., 1992). This high abundance allowed us to locate trees close to the edge of the forest fragments (edge-effect) and also in the interior of the forest (Fig. 7). Trees exposed to edge effects were located close

to the edge (maximum 300 m from any edge) on the Porto Alegre ranch, specifically at the 100-ha Porto Alegre Reserve (2°22'2.82"S, 59°58'31.63"W). The reserve was isolated and created in August 1983, by cutting and burning the surrounding pristine forest to establish new pasture lands. We defined the penetration distance of edge effects as up to 300 m because increasing tree mortality associated with forest fragmentation can be detectable up to this distance (Laurance et al., 1998). Trees not exposed to edge effects were sampled at the Esteio ranch, within continuous forest located on the Km-41 Reserve (2°26'15.52"S, 59°46'1.25"W). Trees were located at least 1,000 m from the nearest edge (a narrow unpaved road). This reserve was created in 1984, and the forest is kept intact and used as one of the control areas.

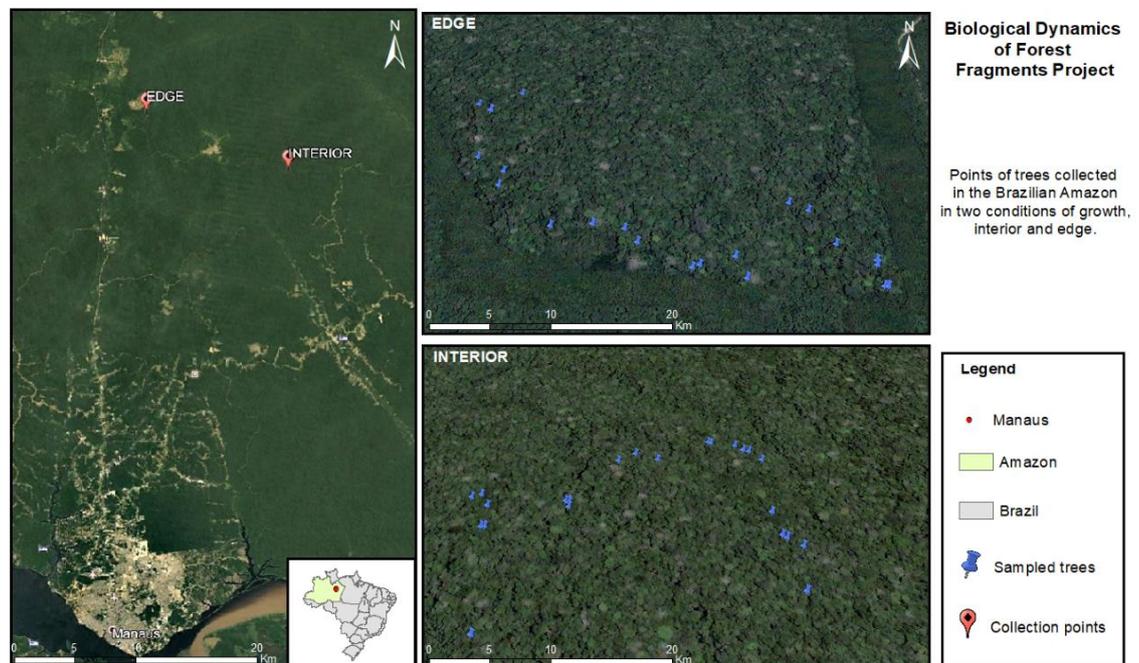


Figure 7. Location (red dots) of the two study sites at the Biological Dynamics of Forest Fragments Project (BDFFP) in terra firme forests of Central Amazonia (left). Blue dots indicate sampled trees in the forest fragment of the Porto Alegre ranch (upper right map).

Tree-ring analyses of *Scleronema micranthum*

For dendroecological analyses we sampled between April and October 2016 a total of 42 *Scleronema micranthum* trees (≥ 10 cm DBH), 21 growing close to the forest edge and 21 in the interior of continuous forest. The species is a canopy tree, rarely semi-deciduous, presenting annual flowering from July to October and fructification from September to February (Alencar et al., 1979).

All sampled trees were in good phytosanitary condition and did not present liana infestation. From each tree, three radial cores were sampled at breast height using increment

borers (diameter = 5.1 mm). Each core was polished with different abrasive sand paper (from 80 to 600 grit/mm²) with the aim of revealing anatomically the growth ring boundary. Subsequently, all tree-rings were identified with the aid of a stereomicroscope according to the Skeleton-plots classic method (Stokes and Smiles, 1996), using narrow rings as guides. After macroscopic identification, all tree-ring series were scanned at a resolution of 2,400 dpi with an HP G4050 scanner. Measurement of ring widths was performed with a precision of 0.001 mm through the software Image J. To evaluate dating accuracy, the temporal series of ring widths were compared within and among trees at each site by visual and statistical cross-dating.

Visual cross-dating was done working with ring-width bar plots, and statistical cross-dating was tested using COFECHA software (Holmes, 1983). COFECHA uses segmented temporal series correlation techniques among series to assess the quality of cross dating and measurement accuracy allowance (Grissino-Mayer, 2001). After evaluating the quality dating control by COFECHA software, we constructed chronologies for each site, trying to retain the common growth variability at high and low frequency ranges, respectively, as much as possible. According to Cook and Kairiukstis (1990), spline functions with a rigidity between 67% and 75% of the series length are an effective tool to remove long-term growth variations resulting from ontogenetic effects and competition between trees in dense forests. To build site chronologies, time series were detrended and standardized using a smoothed cubic spline function with 50% frequency-response (65% cut-off for the length of each series) using the *dplR* package in R Software (Bunn, 2008). Standardization of the series was performed by dividing the width of the growth rings by the growth model of the smooth cubic spline function, producing dimensionless ring-width indices (RW) (Bunn & Korpela, 2017). The quality of the chronology was evaluated by the value of *Rbar* and *EPS* (expressed population signal), both calculated with the *dplR* package in R Software (Bunn, 2008). The *Rbar* is the average correlation coefficient among all the series included in the chronology (Briffa, 1995). The *EPS* values provided information that confirmed the existence of common signals among trees. *EPS* values higher than 0.80 indicate that the limiting factor to growth in the chronology is probably homogenous (Mendivelso et al., 2014).

Growth-climate analyses

To explore growth-climate patterns among trees located close to the edges and trees located in the forest interior, the ring-width data were converted into basal area increment (BAI). BAI is considered a more informative measure of tree growth trends in terms of total

biomass production (Peñuelas et al., 2011; Phipps and Whiton, 1988), to explore the differences in growth-climate patterns between trees located close to the edges and trees located in the forest interior. Ring-width was converted to BAI according to the following standard formula: $BAI = \pi (R_n^2 - R_{n-1}^2)$, where R is the tree radius and n is the growth ring formation year. To calculate BAI we used the `bai.out` function in `dplR` package in R Software (Bunn, 2008; Bunn & Korpela, 2017).

After transforming growth ring width in BAI, we evaluated, by spatial correlations, the influence of sea surface temperature (SST) from the Atlantic (A.SST) and Pacific (P.SST) Oceans on tree BAI using data available from the Climate Explorer Website (<http://climexp.knmi.nl/>) from the KNMI (Royal Netherlands Meteorological Institute), through HadISST1 1.0° special field correlation. Hence, we divided the time series into two periods, prior (1941 to 1982) and after forest fragmentation and, consequently, edge creation (1983 to 2013) analyzing the influence of the period before the dry season (March to June), the period of the core dry season (July to October), and the period after the dry season with the onset of rainfall (November to February).

After verifying the spatial correlations of A.SST and P.SST, a Structural Equation Model (SEM) was used to evaluate how A.SST and P.SST influence the regional rainfall and how these affect the BAI dynamics of trees exposed to edge effects compared to the control for the periods prior, during and after the dry season. Although the application of SEM in dendrochronological research can be considered contemporary, some studies have shown that this technique is a successful statistical tool in verifying climate influence on tree growth (Brienen, et al., 2010; Nielsen et al., 2017; Shi et al., 2018). Using SEM, we were capable of quantifying the direct and indirect causal pathways and the direction (positive or negative) of the influence on tree growth (Grace et al., 2010). In this sense, we used the spatial correlation analyses as hypotheses for the construction of our SEM model, that is, the spatial correlations results found would comprise the paths model. It should be remembered that correlation does not imply causation; however, we were careful to construct a putative causal network that correctly represented the phenomenon. Thus, one of the main advantages of SEM in this study is to allow multiple variables to interact simultaneously, favoring the understanding of the direct rainfall effects and indirect SST effects on tree BAI dynamics.

A general SEM can be expressed in matrix notation as: $y = \Lambda y + \Gamma x + e$, where y is a vector of endogenous variables (whose values are influenced by factors considered in the model); Λ is a square matrix with zeros in the diagonal and structural coefficients in the off-diagonals defining the relations among endogenous variables; Γ is a matrix defining the

relations from exogenous (whose values are influenced by factors ignored by the model) to endogenous variables; x is a vector of exogenous observed variables; and e is a vector of residuals (Rosa et al., 2011).

Historical series (1941 to 2013) of precipitation (CRU TS 4.02, 0.5° - 2.27°-2.47°S and 59°-60°W), North Atlantic SST (NA.SST, 6-22°N and 80-15°W), South Atlantic SST (SA.SST, 25°S-2°N and 35°W-10°E) and El Niño 3.4 P.SST (Niño 3.4, 5°S-5°N and 170°-120°W), obtained from the Climate Explorer Website (<http://climexp.knmi.nl/>) were included as pathways that directly and indirectly influenced tree growth dynamics in the SEM model. According to Yoon and Zeng (2010), the influence of P.SST in the El Niño 3.4 region on Amazonia precipitation presents a lag of 3 to 4 months, thus, the pathways Niño 3.4, presented a lag in the SEM model.

We used the overall test of model fit (chi-square) as well as tests of individual parameters (p value) to estimate the performance of our SEM (Byrne, 2013). The SEM analyses were conducted using R (Lavaan Package) (Rosseel, 2012).

Results

Tree-rings chronologies of *Scleronema micranthum*

The growth rings of *Scleronema micranthum* trees at both sites were distinct and characterized by tangentially distended rays touching the apotracheal, possibly terminal parenchyma bands (Vetter and Botosso, 1988) (Fig. 8). The master chronology (Fig. 9) was built from tree-ring widths covering 138 years (1878–2015) for trees located within the interior of the forest and 142 years (1874–2015) in trees located close to edges. Cross-dating quality and accuracy in the measurements of the growth rings was confirmed by the inter-correlations, $EPS > 0.80$, and $Rbar > 0.3$ values, indicating a common growth pattern of *Scleronema micranthum* at each site, with an evident population signal. Descriptive statistics of the chronologies are presented in Table 4. Results concerning the temporal growth dynamics of the trees exposed, and not exposed to edge effects, can be consulted in (Albiero-Júnior et al., 2019b).



Figure 8. a) *Scleronema micranthum* tree at the forest edge at the Biological Dynamics of Forest Fragments Project site; b) macroscopic, and c) microscopic images of the transverse wood section evidencing the growth ring anatomy characterized by tangentially distended rays touching the apotracheal, possibly terminal parenchymal bands. White triangles indicate the growth-ring boundaries.

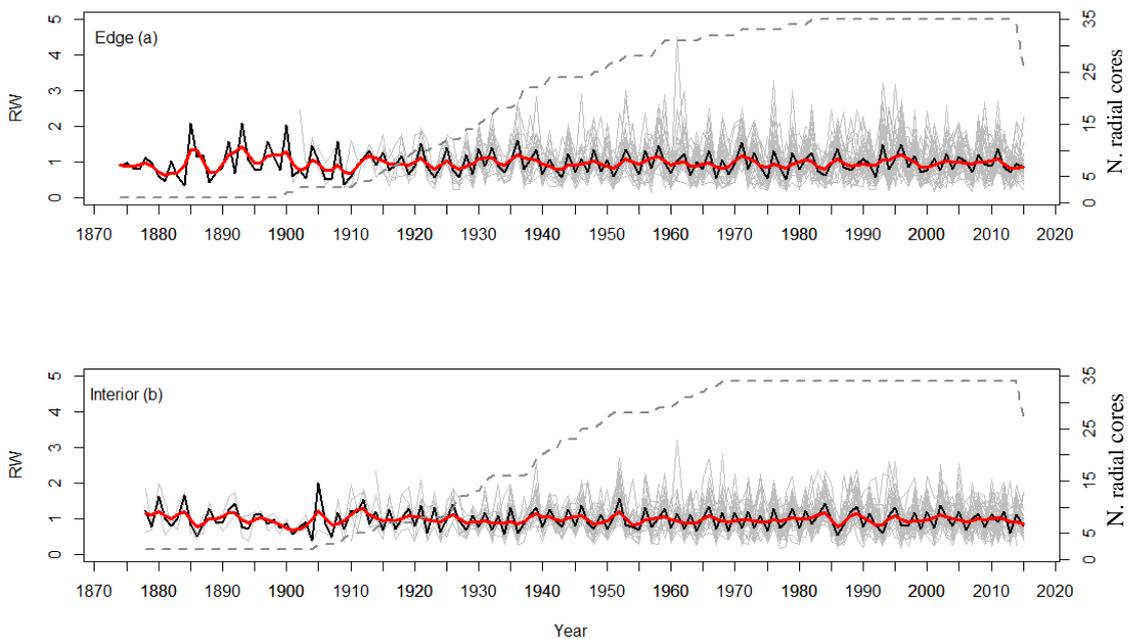


Figure 9. Residual tree-ring chronologies of *Scleronema micranthum* (a) at the forest edge and (b) in intact *terra firme* forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. Solid gray line indicates the individual average time series; the black line shows the residual tree-ring master chronology; the dashed gray line indicates the number of radial cores used for the index calculation and the red line, a superimposed 10%-smoothed spline curve.

Table 4. Descriptive statistics of tree-ring chronologies of *Scleronema micranthum* located close to the edge and in the interior of the reserves at the Biological Dynamics of Forest Fragments Project in Central Amazonia.

Variables	Edge	Interior
No. trees/No. radial cores	21/34	21/34
Mean ring width \pm SD (cm)	0.18 \pm 0.12	0.18 \pm 0.09
Time span	1874-2015	1878-2015
Mean tree age \pm	81 \pm 22	81 \pm 22
Mean sensitivity	0.56	0.51
Series intercorrelation	0.51	0.50
Rbar (\pm SD)	0.44 \pm 0.02	0.36 \pm 0.05
Period with EPS \geq 0.80	1920-2015	1915-2015

Climate-growth analyses

After construction of the two chronologies, we sought to compare climate-growth relations of populations growing at the forest edge and in the interior of the forest. Therefore, we selected 15 trees at each site with similar age and diameter structure comprising the entire period from 1941 to 2014 (Table 5 and Fig. 10). With this we ensure the climate-growth relationship analyses of trees which have been growing in the period before forest fragmentation starting in 1983 and which were influenced by increasing A.SST 1980 onwards. Climate-growth analyses were performed for these subsamples (30 individuals), converting the ring width into basal area increment (BAI).

Table 5. Age and diameter at breast height (DBH) of *Scleronema micranthum* trees at edge and interior of *terra firme* forests at the Biological Dynamics of Forest Fragments Project in Central Amazonia selected for growth pattern analyses (SD indicates the standard deviation).

Year	Edge		Interior	
	DBH	Age	DBH	Age
1941	6.9 (SD = 5.8)	20 (SD = 17)	6.9 (SD = 6.2)	23 (SD = 18.2)
1982	22.3 (SD = 6.3)	61 (SD = 17)	22.1 (SD = 7.1)	64 (SD = 19)
2014	33.3 (SD = 5.2)	92 (SD = 17.8)	34.9 (SD = 6.7)	96 (SD = 12.2)

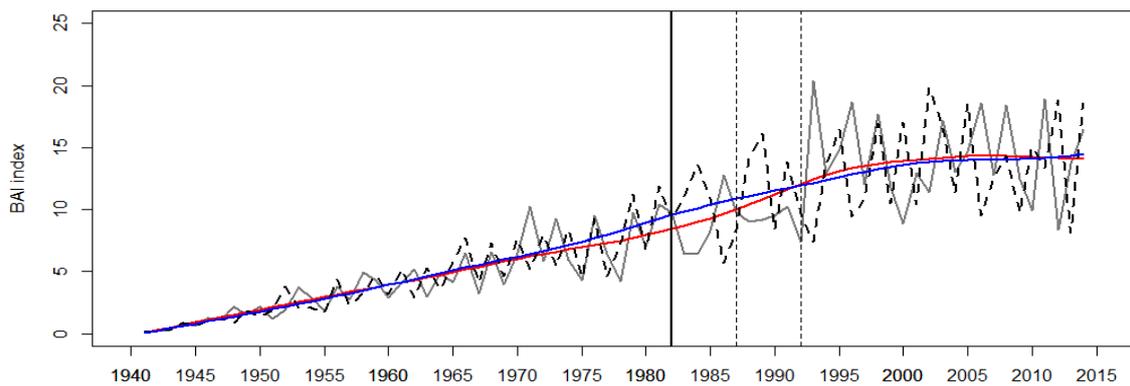


Figure 10. Dominant basal area increment (BAI) index patterns of *Scleronema micranthum* trees located close to the edge (solid gray lines) and in the interior of the forest (dashed black line) in *terra firme* forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. Red line: standardization by a 30% smoothed spline curve of BAI chronology of trees located close to the edge; blue line: standardization by a 30% smoothed spline curve of BAI chronology of trees in the interior of the forest; vertical solid black line: edge creation year (1982); vertical dashed black line: five and ten years after edge creation.

Spatial correlations evidenced strong influence of A.SST on tree growth inside the forest (Fig. 11) and at the forest edge (Fig. 12). Both populations show a changing pattern from the SA.SST influencing tree growth during the period before forest fragmentation towards NA.SST influencing tree growth in the period afterwards. The strength and fields of correlations of SA.SST patterns before forest fragmentation are very similar between both populations, however after forest fragmentation and increased A.SST since 1980, the populations present differences especially during the core period of the dry season (Jul – Oct–Oct), with stronger influence of NA.SST on the trees growing at the forest edge. The influence of P.SST in the El Niño 3.4 region is relatively low and more evident during the core period of the dry season, especially for the population in intact forests in the period before forest fragmentation.

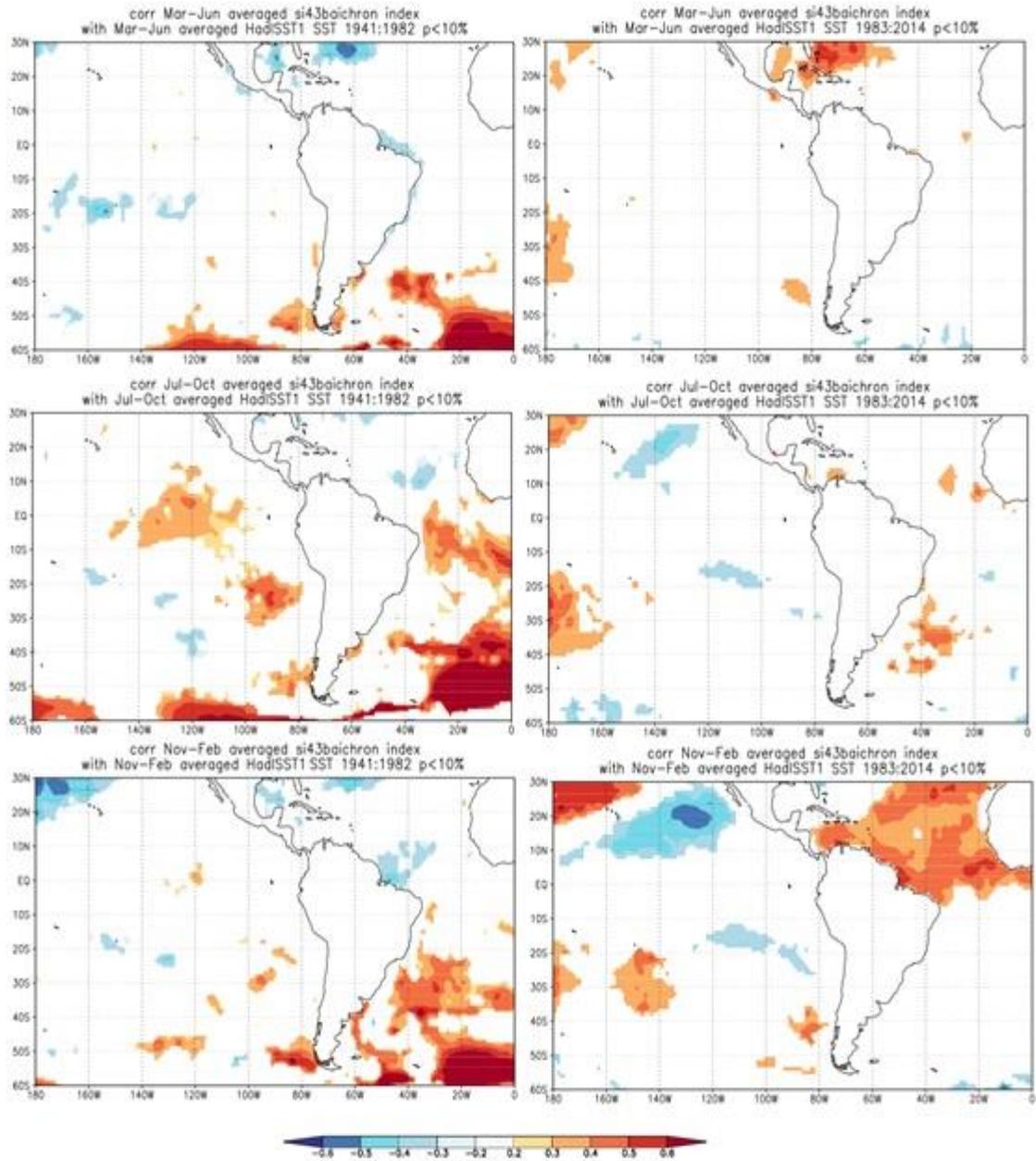


Figure 11. Spatial correlations between the Atlantic sea surface temperature (A.SST) and the basal area increment (BAI) of *Scleronema micranthum* trees not exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia, before (left side) and after (right side) forest fragmentation, considering the period before (Mar – Jun), during (Jul – Oct) and after (Nov – Feb) the dry season.

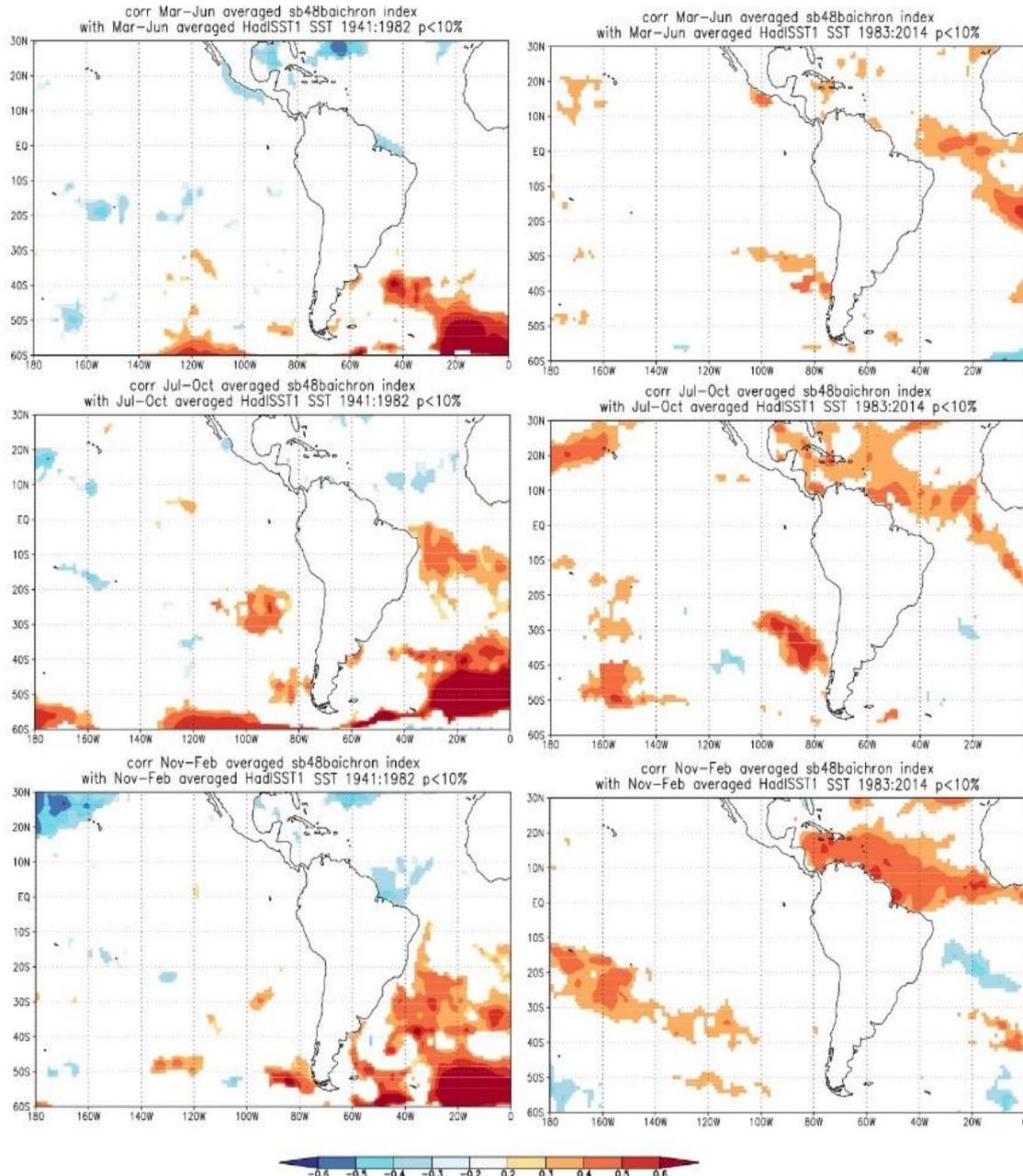


Figure 12. Spatial correlations between the Atlantic sea surface temperature (A. SST) and the basal area increment (BAI) of *Scleronema micranthum* trees exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia, before (left side) and after (right side) forest fragmentation considering the period before (Mar – Jun), during (Jul – Oct) and after (Nov – Feb.) the dry season.

The structural Equation Model (Fig. 13) revealed, with statistical significance, Chi-Square P -value >0.05 , the direct influence of precipitation and indirect influence of the SA.SST, NA.SST and P.SST El Niño 3.4 variables on BAI rates. The variables included in the structural models represent annual average rates, thus, the interpretation of the paths corresponds to the average influence that one variable had on the others during the time under consideration.

For trees located in the interior forest, we observed that rainfall rates positively affected the basal growth rate before fragmentation during the periods of Mar - Jun and Jul - Oct. Basal growth rates increased as the mean rainfall increased (Fig. 13). However, the rainfall rate during the period of Nov – Feb had a negative effect on basal growth rate. After forest fragmentation and as A.SST increased, the rainfall rate had a negative influence on BAI rates of interior trees during the periods of Jul – Oct and Nov – Feb. However, the effects of rainfall were lower and not significant during and after the core of the dry season. During the period from March to June prior to the dry season, rainfall positively influenced BAI rate of interior trees.

After forest fragmentation and as A.SST had increased, we observed an interesting phenomenon. The rainfall rate of Jul – Oct (-0.008 cm^2) and Nov – Feb (-0.006 cm^2) periods, had a negative influence on BAI rates of interior trees; thus, as the rainfall rate during these periods increased, the BAI rate decreased. However, values close to zero may indicate that rainfall during and after the core of the dry season exerted little influence on the growth of trees located in the forest interior after 1983. Prior to the dry season, rainfall from March to June continued to positively influence the growth of trees located in the forest interior after forest fragmentation and increased A.SST, inducing increases in BAI rates of 0.020 cm^2 per year.

For trees located close to the edges, the effects of rainfall rates on basal growth rate before forest fragmentation was the same as that of trees located in the interior of the forest. However, after forest fragmentation and increased A.SST since 1980, we observed that trees exposed to edge effects were much more sensitive to rainfall reduction in the core of the dry season (Jul – Oct) period, presenting an almost ninefold decrease (-0.070 cm^2) of BAI than trees at the control site. On the other hand, the effect of rainfall before and after the core of the dry season after forest fragmentation remained similar to trees located in the interior of the forest, with a BAI increasing close to 0.025 cm^2 in the period of Mar – Jun and almost null (0.005 cm^2) in the period of Nov – Feb.

Analyzing the indirect effect of large-scale climatic variables (SA.SST, NA.SST, and P.SST El Niño 3.4) on precipitation that influenced the trees not exposed to edge effects before A.SST increase and forest fragmentation, SEM revealed a rainfall increase from Mar – Jun and Jul – Oct, and a reduction during Nov – Feb and Mar – Jun (Niño 3.4). This revealed, before the A.SST increased and forest fragmentation, a positive influence of SA.SST on precipitation before and during the dry season, and negative influences of El Niño 3.4 and SA.SST during and after the core of the dry season, respectively.

This large-scale climate pattern was similar for trees close to the edge before forest fragmentation and increased A.SST, except for the absence of P.SST El Niño 3.4 influence which was not observed in the spatial correlation analysis of the edge trees.

In the period after A.SST increased and forest fragmentation, the Atlantic sea surface temperatures exerted a lower influence on the precipitation available for the trees distant from the edge, presenting negative correlation with SA.SST during Jul – Oct and with NA.SST during Nov – Feb. For trees growing close to the forest edge, the influence of Atlantic sea surface temperatures, mainly the NA.SST, was much stronger compared to the control, causing a strong reduction of rainfall during Jul – Oct and Nov – Feb and a lower decrease in Mar – Jun (Fig. 13).

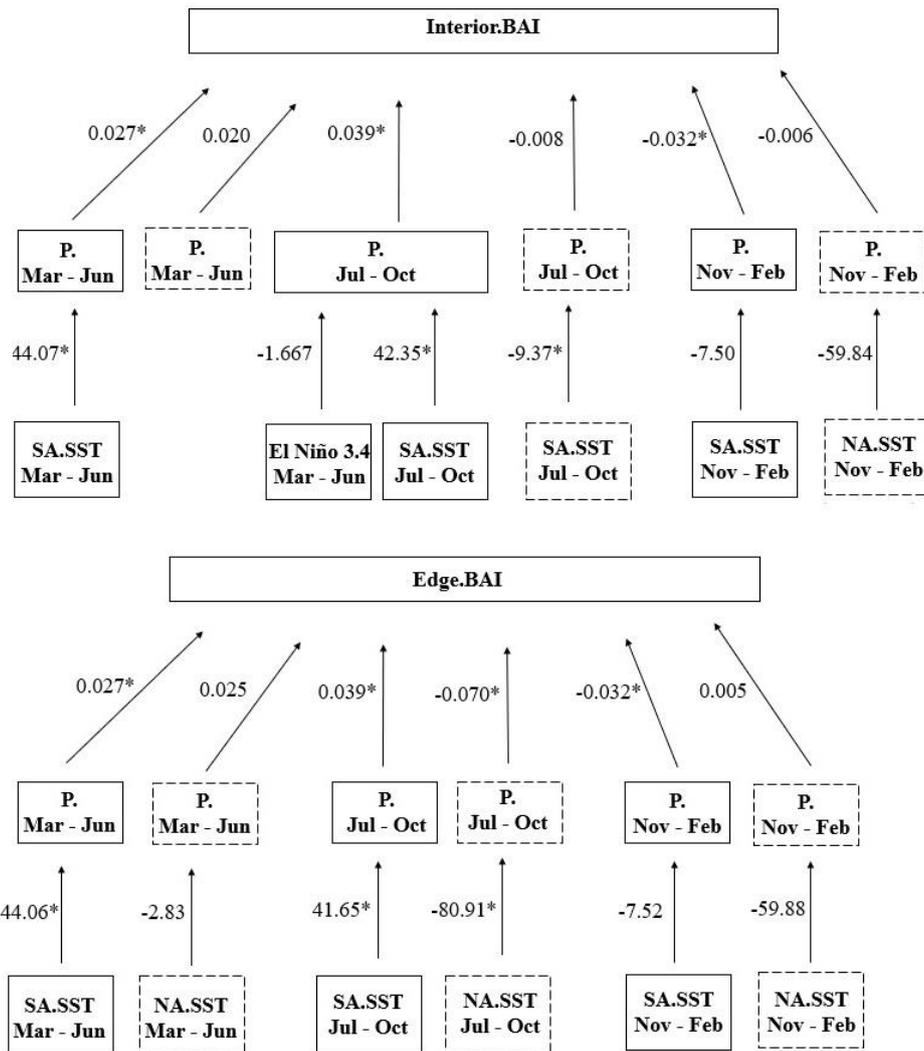


Figure 13. Structural Equation Model of climate-growth relationships for trees not exposed (Interior.BAI) and exposed (Edge.BAI) to edge effects for the periods before (Mar – Jun), during (Jul – Oct) and after (Nov – Feb) the dry season. Solid boxes represent data prior to forest fragmentation, and dashed boxes represent data after forest fragmentation. The asterisks indicate significance of the path ($p < 0.05$). (P: precipitation, SA.SST: South Atlantic sea surface temperature; NA.SST: North Atlantic sea surface temperature; El Niño 3.4: Pacific sea surface temperature in El Niño 3.4 region).

Discussion

The spatial-temporal variability observed in the correlations between BAI rates and A.SST (Figs. 11 and 12) revealed a stronger influence of SA.SST in the period before forest fragmentation, and NA.SST after forest fragmentation.

This switch effect from the SA.SST to the NA.SST is possibly caused by a displacement of the Intertropical Convergence Zone (ITCZ) towards the north due to the increases in A.SST from 1980 onward (Gloor et al., 2013, 2015). Through the A.SST increase and the consequent displacement of ITCZ to the north, an intensification of the hydrological

cycle in the wet season and small reductions in rainfall during the dry season are expected (Gloor et al., 2013; Marengo et al., 2008; Yoon and Zeng, 2010). Consequences of this phenomenon, in which the temperature increase of A.SST induced the displacement of the ITCZ to the north, promoting rainfall reduction, were observed in intense drought years (1998, 2005 and 2010) in the Western Amazon (Espinoza et al., 2011), and it was reported that this phenomenon has promoted high tree mortality and biomass loss (Feldpausch et al., 2016; Laurance et al., 2001; Phillips et al., 2009), affecting the dynamics of the forest and consequently its ecosystem services. Thus, although the intensification of the hydrological cycle in the Amazon since 1980 onward (Gloor et al., 2013, 2015) could indicate that trees of *terra firme* forests would benefit from increases rainfall, and would be little affected by the small reductions in rainfall during the dry season, only boosting water stress in areas of shallow soils in Amazonia (Gloor et al., 2015). The negative values found by the path P.Jul.Oct (-0.070 cm²) → Edge.BAI on SEM edge model (Fig. 13) after forest fragmentation and increased A.SST since 1980, reveals that even in areas with deep soils, such as the Ferralsols (Oxisol) characteristic in our study area, which favors a root depth of trees of up to two meters (Quesada et al., 2011). Dry periods, slightly drier, may potentiate stress conditions (e.g., increases in air temperature, reduction of air humidity and soil moisture) already observed in edge areas, contributing even more to the reduction of tree growth.

In addition, when we observed that the increase of NA.SST from July to October exerted strong pressure on the reduction of rainfall during the dry season (-80.91 mm) in the edge SEM model (Fig. 8), we can expect that the reduction of forest cover in fragmented areas may be potentiating the reduction of rainfall during the dry season, since 25% of rainfall in the Amazon is recycled from the forest itself (Angelini et al., 2011). In this sense, recognizing the key role of forest cover in the hydrological cycle, directly influencing climate (Bonan, 2008), and the displacement of ITCZ to the north due to the increase of A.SST since 1980, we can expect that macro- and microclimatic changes are acting as the factors to reduce rainfall in fragmented areas of the Amazon forest, especially during the drier period, as revealed by the greater sensitivity to climate changes in *Scleronema micranthum* trees exposed to edge effects.

Consequently, if we consider the projections of 1.5 °C global warming above pre-industrial levels (Intergovernmental Panel on Climate Change 2019), significant increases in A.SST will possibly modify rainfall patterns in the Amazon Basin even more. This will influence the performance of trees and their ecosystem services, especially in forest areas that already undergo stress at the edges of forest fragments. This was observed in trees of *S.*

micranthum exposed to edge effects, that presented, during the first 10 years of forest fragmentation (1983 to 1992), an 18% reduction of BAI rates (Albiero-Júnior et al., 2019).

Surprisingly, for the period with onset of rainfall (Nov – Feb), the SEM model suggests a reduction of tree growth of *S. micranthum* for both populations (forest edge and continuous forest), contradicting dendroclimatological studies performed in tropical forests that demonstrated a positive influence of precipitation at the beginning of the rainy season on tree growth (Brienen & Zuidema, 2005; Dunisch et al., 2003; Granato-Souza et al., 2018). A reasonable explanation for this reduction in *S. micranthum* tree growth would be the influence of cloud formation during the rainy season, reducing light availability and intensity that would reach the canopy, and consequently decrease the photosynthetically active radiation (PAR) available to the trees (Clark and Clark, 1994; Lovejoy and Schertzer, 2006; Soliz-Gamboa et al., 2011).

During the rains that occurred before the core of the dry season, positive and similar correlations (0.027 cm^2) with BAI of trees exposed and not exposed to edge effects observed by the SEM models, may suggest that the last rain events prior to the dry season can be used as an additional resource for tree growth. This result was also observed in tropical forests by Fontana et al. (2018), Brienen and Zuidema (2005) and Dünisch et al. (2003) and may reflect a trade-off between a last growth impulse before the dry season or energy storage for the next growing season (Dunisch et al., 2003). Thus, these responses seem to be exerting the same influence on trees exposed and not exposed to edge effects, before and after forest fragmentation and increased A.SST since 1980, revealing a certain dependence of *S. micranthum* trees on rains prior to the dry season.

Before forest fragmentation, the positive influence of the SA.SST in precipitation from March to June on edge and interior trees, and July to October on trees close to edge, may reflect the colder conditions of the SA.SST before the observed warming since 1980, which according to Yoon and Zeng (2010) would favor ITCZ permanence in its regular position, accentuating rainfall in the Amazon Basin mainly from May to June, corroborating our results. On the other hand, negative and smaller relationships between SA.SST and precipitation from November to February may reflect the low influence of SA.SST during this period, acting, according to Gloor et al. (2015) more intensely in the rains that occur during the transition from the wet to the dry period, as we observed in the Structural Equation Model analysis.

Although Yoon and Zeng (2010) showed strong influence of P.SST on precipitation during the rainy season in the Amazon Basin, recent studies (Barichivich et al., 2018; Gloor et

al., 2013) provide evidence that the Atlantic is the triggering force influencing precipitation in this period, corroborating the lower influence of P.SST observed by the spatial correlations and in the SEM model.

Therefore, we highlight the Atlantic Ocean's determining role in terms of hydroecological impacts due to its influence on rainfall patterns mainly during the dry season in Central Amazonia, and reinforce that increases in A.SST since 1980 might increase the vulnerability to rainfall reduction in trees exposed to edge effects. Legitimate strategies are needed to reduce and mitigate the expansion of edge areas in Amazon forest and anthropic climate changes of the Anthropocene.

Conclusion

The present study was able to identify that Atlantic sea surface temperature (A.SST) increased since 1980 and the Intertropical Convergence Zone northward displacement exerted greater pressures on the growth dynamics of trees exposed to the forest edge, and that these influences were more intense during the dry season. Thus, although we could believe that trees in upland forests (*terra firme*) could benefit from the intensification of the hydrological cycle since 1980, this phenomenon may not favor trees exposed or close to forest edge, mainly in the dry season. Also, this study reinforces the anticorrelation phenomenon of A.SST increase and rainfall reduction in the Amazon, and highlight that in altered and potentially more stressful environments, such as forest edges, Anthropocene climatic changes may be exerting pressure on reducing the growth dynamics of the trees. This is able to alter essential processes (flowering, fruiting and growth) in their ecosystem services that can affect human well-being. Therefore, through dendrochronology we legitimize the claims that climatic changes and Amazon fragmentation are exerting a strong impact on *Scleronema micranthum* growth dynamics, highlighting the need for strategies that reduce forest fragmentation and creation of new forest edges.

Acknowledgements

This work was funded by the Rufford Small Grant for Nature Conservation (<http://www.rufford.org/>, RSGA application 18762-1), BDFFP's Thomas Lovejoy research fellowship program and conducted during a scholarship supported by the International Cooperation Program CAPES/PVE (process: 88887.127558/2016-00) at Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Mendoza, Argentina. The first author was supported by a Ph.D. scholarship from CAPES – Brazilian Federal Agency

for the Improvement of Higher Education Personnel. This is publication number 763 of the Biological Dynamics of Forest Fragments Project (BDFFP – INPA/STRI) Technical Series.

References

- Albiero-Júnior, A., Venegas-González, A., Botosso, P.C., Roig, F.A., Camargo, J.L.C., Tomazello-Filho, M., 2019. What is the temporal extension of edge effects on tree growth dynamics? A dendrochronological approach model using *Scleronema micranthum* (Ducke) Ducke trees of a fragmented forest in the Central Amazon. *Ecol. Indic.* 101, 133–142.
- Alencar, J. da C., de Almeida, R.A., Fernandes, N.P., 1979. Fenologia de espécies florestais em floresta tropical úmida de terra firme na Amazônia Central. *Acta Amaz.* 9, 163–199.
- Angelini, I.M., Garstang, M., Davis, R.E., Hayden, B., Fitzjarrald, D.R., Legates, D.R., Greco, S., Macko, S., Connors, V., 2011. On the coupling between vegetation and the atmosphere. *Theor. Appl. Climatol.* 105, 243–261.
- Barichivich, J., Gloor, E., Peylin, P., Brienen, R.J.W., Schöngart, J., Espinoza, J.C., Pattanayak, K.C., 2018. Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. *Sci. Adv.* 4, 8785–8793.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science.* 320, 1444–1449.
- Brienen, R.J.W., Lebrija-Trejos, E., Zuidema, P.A., Martínez-Ramos, M., 2010. Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. *Glob. Chang. Biol.* 16, 2001–2012.
- Brienen, R.J.W., Schöngart, J., Zuidema, P.A., 2016. Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees, in: *Tropical Tree Physiology*. Springer, pp. 439–461.
- Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146, 1–12.
- Briffa, K.R., 1995. Interpreting high-resolution proxy climate data—the example of dendroclimatology, in: *Analysis of Climate Variability*. Springer, pp. 77–94.
- Bunn, A., Korpela, M., 2017. An introduction to dplR.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124.
- Byrne, B.M., 2013. Structural equation modeling with Mplus: Basic concepts, applications, and programming. Routledge.

- Callede, J., Cochonneau, G., Vieira Alves, F., Guyot, J.-L., Santos Guimaraes, V., De Oliveira, E., 2010. The river amazon water contribution to the atlantic Ocean. *Rev. des Sci. l'eau*. 23, 197–323.
- Camargo, J.L.C., Kapos, V., 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* 11, 205–221.
- Clark, D.A., Clark, D.B., 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. *J. Ecol.* 82, 865–872.
- Cook, E.R., Kairiukstis, L.A., 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer, Amsterdam.
- Crutzen, P.J., Stoermer, E.F., 2000. The “Anthropocene.” *Global Change Newsletter*. 41, 17–18.
- Dunisch, O., Montoia, V.R., Bauch, J., 2003. Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. *Trees-Structure Funct.* 17, 244–250.
- Espinoza, J.C., Ronchail, J., Guyot, J.L., Junquas, C., Vauchel, P., Lavado, W., Drapeau, G., Pombosa, R., 2011. Climate variability and extreme drought in the upper Solimões River (western Amazon Basin): Understanding the exceptional 2010 drought. *Geophys. Res. Lett.* 38, 1–6.
- Fauset, S., Johnson, M.O., Gloor, M., Baker, T.R., Monteagudo, A., Brienen, R.J.W., Feldpausch, T.R., Lopez-Gonzalez, G., Malhi, Y., Ter Steege, H., 2015. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* 6, 1–9.
- Fearnside, P.M., 1997. Environmental services as a strategy for sustainable development in rural Amazonia. *Ecol. Econ.* 20, 53–70.
- Feldpausch, T.R., Phillips, O.L., Brienen, R.J.W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Alarcón, A., Álvarez Dávila, E., 2016. Amazon forest response to repeated droughts. *Global Biogeochem. Cycles* 30, 964–982.
- Fontana, C., Pérez-de-Lis, G., Nabais, C., Lousada, J.L.P.C., Olmedo, G.M., Botosso, P.C., Oliveira, J.M., 2018. Climatic signal in growth-rings of *Copaifera lucens*: an endemic species of a Brazilian Atlantic Forest hotspot, southeastern Brazil. *Dendrochronologia* 50, 23–32.
- Gascon, C., Bierregaard Jr, R.O., 2001. The biological dynamics of forest fragments project. *Lessons from Amazonia: The ecology and conservation of a fragmented forest*. 31–42.

- Gloor, M., Barichivich, J., Ziv, G., Brienen, R., Schöngart, J., Peylin, P., Cintra, L., Barcante, B., Feldpausch, T., Phillips, O., 2015. Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. *Global Biogeochem. Cycles* 29, 1384–1399.
- Gloor, M., Brienen, R.J.W., Galbraith, D., Feldpausch, T.R., Schongart, J., Guyot, J.L., Espinoza, J.C., Lloyd, J., Phillips, O.L., 2013. Intensification of the Amazon hydrological cycle over the last two decades. *Geophys. Res. Lett.* 40, 1729–1733.
- Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. *Ecol. Monogr.* 80, 67–87.
- Granato-Souza, D., Stahle, D.W., Barbosa, A.C., Feng, S., Torbenson, M.C.A., de Assis Pereira, G., Schöngart, J., Barbosa, J.P., Griffin, D., 2018. Tree rings and rainfall in the equatorial Amazon. *Clim. Dyn.* 52, 1857–1869.
- Grissino-Mayer, H.D., 2001. Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. *Tree-Ring Res.* 57, 205–221.
- Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of monthly climatic observations—the CRU TS3. 10 Dataset. *Int. J. Climatol.* 34, 623–642.
- Hilker, T., Lyapustin, A.I., Tucker, C.J., Hall, F.G., Myneni, R.B., Wang, Y., Bi, J., de Moura, Y.M., Sellers, P.J., 2014. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proc. Natl. Acad. Sci.* 111, 16041–16046.
- Hoegh-Guldberg, O. et al. in *Special Report: Global Warming of 1.5°C* Ch. 3 (eds Masson-Delmotte, V. et al.) (IPCC, 2019).
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43, 69–78.
- Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., Meyer, C.F.J., Bobrowiec, P.E.D., Laurance, S.G.W., 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biol. Rev.* 93, 223–247.
- Laurance, W.F., Ferreira, L. V, Rankin-de Merona, J.M., Laurance, S.G., 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79, 2032–2040.
- Laurance, W.F., Williamson, G.B., Delamônica, P., Oliveira, A., Lovejoy, T.E., Gascon, C., Pohl, L., 2001. Effects of a strong drought on Amazonian forest fragments and edges. *J. Trop. Ecol.* 17, 771–785.

- Lovejoy, S., Schertzer, D., 2006. Multifractals, cloud radiances and rain. *J. Hydrol.* 322, 59–88.
- Makarieva, A.M., Gorshkov, V.G., Li, B.-L., 2013. Revisiting forest impact on atmospheric water vapor transport and precipitation. *Theor. Appl. Climatol.* 111, 79–96.
- Malcolm, J.R., 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Clim. Change* 39, 487–502.
- Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Glob. Chang. Biol.* 12, 1107–1138.
- Marengo, J.A., 2006. On the hydrological cycle of the Amazon Basin: A historical review and current state-of-the-art. *Rev. Bras. Meteorol.* 21, 1–19.
- Marengo, J.A., Espinoza, J.C., 2016. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. *Int. J. Climatol.* 36, 1033–1050.
- Marengo, J.A., Nobre, C.A., Tomasella, J., Cardoso, M.F., Oyama, M.D., 2008. Hydro-climatic and ecological behaviour of the drought of Amazonia in 2005. *Philos. Trans. R. Soc. London B Biol. Sci.* 363, 1773–1778.
- Mendivelso, H.A., Camarero, J.J., Gutiérrez, E., Zuidema, P.A., 2014. Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity. *Agric. For. Meteorol.* 188, 13–23.
- Nielsen, S.S., Arx, G. von, Damgaard, C.F., Abermann, J., Buchwal, A., Büntgen, U., Treier, U.A., Barfod, A.S., Normand, S., 2017. Xylem anatomical trait variability provides insight on the climate-growth relationship of *Betula nana* in western Greenland. *Arctic, Antarct. Alp. Res.* 49, 359–371.
- Nobre, C.A., Obregón, G.O., Marengo, J.A., Fu, R., Poveda, G., 2009. Características do clima amazônico: Aspectos principais. *Am. Geophys. Union.* 186, 149–162.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* 20, 597–608.
- Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., 2009. Drought sensitivity of the Amazon rainforest. *Science.* 323, 1344–1347.
- Phipps, R.L., Whiton, J.C., 1988. Decline in long-term growth trends of white oak. *Can. J. For. Res.* 18, 24–32.

- Pinto, S.R.R., Mendes, G., Santos, A.M.M., Dantas, M., Tabarelli, M., Melo, F.P.L., 2010. Landscape attributes drive complex spatial microclimate configuration of Brazilian Atlantic forest fragments. *Trop. Conserv. Sci.* 3, 389–402.
- Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon.
- Quesada, C.A., Lloyd, J., Anderson, L.O., Fyllas, N.M., Schwarz, M., Czimczik, C.I., 2011. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*. 8, 1415–2011.
- Rankin-de-Mérona, J.M., Prance, G.T., Hutchings, R.W., Silva, M.F. da, Rodrigues, W.A., Uehling, M.E., 1992. Preliminary results of a large-scale tree inventory of upland rain forest in the Central Amazon. *Acta Amaz.* 22, 493–534.
- Roosevelt, A.C., 2013. The Amazon and the Anthropocene: 13,000 years of human influence in a tropical rainforest. *Anthropocene* 4, 69–87.
- Rosa, G.J.M., Valente, B.D., de los Campos, G., Wu, X.-L., Gianola, D., Silva, M.A., 2011. Inferring causal phenotype networks using structural equation models. *Genet. Sel. Evol.* 43, 1–13.
- Rosseel, Y., 2012. Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA). *J. Stat. Softw.* 48, 1–36.
- Saatchi, S.S., Houghton, R.A., Dos Santos Alvala, R.C., Soares, J.V., Yu, Y., 2007. Distribution of aboveground live biomass in the Amazon basin. *Glob. Chang. Biol.* 13, 816–837.
- Shi, F., Wu, X., Li, X., Chen, D., Liu, H., Liu, S., Hu, X., He, B., Shi, C., Wang, P., 2018. Weakening relationship between vegetation growth over the Tibetan Plateau and large-scale climate variability. *J. Geophys. Res. Biogeosciences* 123, 1247–1259.
- Sizer, N., Tanner, E.V.J., 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biol. Conserv.* 91, 135–142.
- Soliz-Gamboa, C.C., Rozendaal, D.M.A., Ceccantini, G., Angyalossy, V., van der Borg, K., Zuidema, P.A., 2011. Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees. *Trees-Structure Funct.* 25, 17–27.
- Stohl, A., James, P., 2005. A Lagrangian analysis of the atmospheric branch of the global water cycle. Part II: Moisture transports between earth's ocean basins and river catchments. *J. Hydrometeorol.* 6, 961–984.
- Stokes, M.A., Smiles, T., 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.

- Ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C. V, Magnusson, W.E., Molino, J.-F., 2013. Hyperdominance in the Amazonian tree flora. *Science*. 342, 325–337.
- Thompson, S.C.G., Barton, M.A., 1994. Ecocentric and anthropocentric attitudes toward the environment. *J. Environ. Psychol.* 14, 149–157.
- Venegas-González, A., Roig, F.A., Lisi, C.S., Albiero-Junior, A., Alvares, C.A., Tomazello-Filho, M., 2018. Drought and climate change incidence on hotspot Cedrela forests from the Mata Atlântica biome in southeastern Brazil. *Glob. Ecol. Conserv.* 15, 1–15.
- Vetter, R.E., Botosso, P.C., 1988. Observações preliminares sobre a periodicidade e taxa de crescimento em árvores tropicais. *Acta Amaz.* 18, 189–196.
- Wang, H., Fu, R., 2007. The influence of Amazon rainfall on the Atlantic ITCZ through convectively coupled Kelvin waves. *J. Clim.* 20, 1188–1201.
- Wesselingh, F.P., Hoorn, C., Kroonenberg, S.B., Antonelli, A., Lundberg, J.G., Vonhof, H.B., Hooghiemstra, H., 2010. On the origin of Amazonian landscapes and biodiversity: a synthesis. *Amaz. Landsc. Species Evol. A look into past* 419–431.
- Worbes, M., 1995. How to measure growth dynamics in tropical trees - A review. *Iawa J.* 16, 337–351.
- Yoon, J.-H., Zeng, N., 2010. An Atlantic influence on Amazon rainfall. *Clim. Dyn.* 34, 249–264.
- Zemp, D.C., Schleussner, C.-F., Barbosa, H.M.J., Van der Ent, R.J., Donges, J.F., Heinke, J., Sampaio, G., Rammig, A., 2014. On the importance of cascading moisture recycling in South America. *Atmos. Chem. Phys.* 14, 13337–13359.
- Zeng, N., Yoon, J.-H., Marengo, J.A., Subramaniam, A., Nobre, C.A., Mariotti, A., Neelin, J.D., 2008. Causes and impacts of the 2005 Amazon drought. *Environ. Res. Lett.* 3, 14002–14011.

Chapter 3

NOT EVERYTHING IS SO BAD: TREE GROWTH UNDER CANOPY OF TERRA FIRME FOREST IN CENTRAL AMAZONIA IS FAVORED AFTER FOREST FRAGMENTATION

Submitted to the journal: Journal of Ecology

Alci Albiero-Júnior^a; Alejandro Venegas-González^b; José Luís Campana Camargo^c; Fidel Alejandro Roig^{d,e,b,a}; Mario Tomazello-Filho^a

^aUniversity of São Paulo, Luiz de Queiroz College of Agriculture, Department of Forest Sciences, Wood Anatomy and Tree-Ring Laboratory, Av. Pádua Dias 11, P.O. Box 9, 13418-900 Piracicaba, SP, Brazil

^bHémera Centro de Observación de la Tierra, Escuela de Ingeniería Forestal, Facultad de Ciencias, Universidad Mayor, Santiago 8340589, Chile

^cBiological Dynamics of Forest Fragments Project (BDFFP), Manaus, AM, Brazil

^dLaboratorio de Dendrocronología e Historia Ambiental, IANIGLA, CCT CONICET Mendoza, CC 330, M5502IRA, Argentina

^eFacultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Almirante Brown 500, Mendoza Argentina

* Corresponding author: albierojunior@usp.br

Abstract

The contemporary socioenvironmental conjuncture of the Brazilian Amazonian, marked by land use conversion, habitat reduction, forest fragmentation and biodiversity loss has been revealing a failure of our society in the maintenance of environmental services provided by the world's largest rainforest. Highlighting the key role of the forest and more precisely of the trees, it's major component may help to understand at least part of the future of a fragmented landscape. More precisely, understanding how tropical trees occupying distinct positions in the forest vertical profile are being affected and reacted to forest fragmentation during their life's cycle will provide more truly insights on the resilience of the Amazonian forest. In this sense, through dendrochronological analyzes, using tree rings as bioindicators, we evaluated the temporal influence of the edge effects on *Theobroma sylvestre* Mart. (Malvaceae) tree growth dynamics, a typical tree that occupy lower and intermediate positions in a forest vertical profile. Dendrochronology surely was a technique that helped us to investigate along time the effects of environmental changes in a natural system and even further, for those survivors' trees in such disturbed environment, how the process of resilience may perform after disturbance. Our dendrochronological study revealed that edge effects favored the growth of *Theobroma sylvestre* trees, mainly along the first 20 years after forest

fragmentation and edge creation. An opposite pattern when compared to the growth dynamics of a canopy tree. Confirming that the microclimatic and structural changes provoked by edge effects exert contrasting influences on trees growth, depending on their position in the forest vertical profile. In addition, we highlighted that the increase in basal area increment of trees in lower and intermediate forest vertical profile exposed to edge effects, may indicate an important component of above ground biomass stocks recover after forest fragmentation. A fact that should be taking into account in forest management and restoration practices. Promoting new perspective to forest resilience ability after fragmentation processes. However, we also highlighted the need of extending the study to a larger number of tree species, to confirm these hypotheses.

Keywords: Amazonian forest fragmentation; Basal area increment; Biological Dynamics of Forest Fragments Project; Growth release; Resilience; Sub-canopy; Tree rings

Introduction

The human well-being is a corollary of the Amazonian forest conservation due to its indispensable contribution for the global carbon cycle (Malhi et al., 2006; Saatchi, Houghton, Alvala, Soares, & Yu, 2007), through the photosynthetic fixation of 17% of the terrestrial carbon biomass (Fauset et al., 2015), also responsible with ~17% of total global freshwater input to the ocean (Callede et al., 2010) and its participation in the energy balance and climate maintenance of the planet (Wang and Fu, 2007; Hilker et al., 2014).

Trees play a key role in the perennity of such environmental services (Lutz et al., 2018; Teixeira et al., 2019). In this sense, considering the increase of Brazilian Amazonian forest deforestation by approximately 88% compared to 2018 (INPE, 2019), and the ongoing potential increases of legal deforestation after Brazilian Forest Act revision, in which favors the reduction size of the legal reserves of private properties from 80% to 50% in Amazonia (Freitas et al., 2018). We highlight the importance of studies evaluating the temporal influence of anthropic (e.g forest fragmentation and climate changes) actions along the trees' live cycle being fundamental to understanding the forest ecosystems dynamics and forest resilience (Gunderson, 2000). Providing, crucial knowledge in planning mitigation and adaptation strategies to the consequences of forest fragmentation (Berenguer et al., 2018) and environmental services conservation.

Recent studies realized in Amazonia using remote sensing techniques, revealed that after selecting logging, the forest understory structure resembled its original state within four to five years while differences in canopy structure were still detected eight years following logging (Rangel-Pinag e et al., 2019). Also using remote sensing techniques, de Paula et al. (2016) observed that tree cover patterns remained in average lower close to the edge after five years of forest fragmentation in Amazonia. Moreover, and through dendrochronological

analysis, Albiero-Junior et al. (2019) registered that Amazonian canopy trees took at least 10 years to record a basal area increment rates similar to those observed in canopy trees not exposed to edge effects.

Studies suggest that tropical forests can take 30 years on average to recover an original level of biomass after forest fragmentation (Letcher and Chazdon, 2009; Poorter et al., 2016; Almeida et al., 2019). However, Berenguer et al. (2018) identified the absence of significant differences in the average wood density of saplings between disturbed mature and secondary Amazonian forests, possibly indicating a process of secundarization (Scarano & Ceotto, 2015), which would lead to the absence of divergences in above ground biomass values in mature and secondary Amazonian forest in future. This homogenization after forest fragmentation, was already registered by Tabarelli et al. (2008) in tropical forest fragments, supporting the hypothesis that assemblages dominated by pioneer trees, may be approaching near-equilibrium conditions, representing a stagnant rather than a transient successional stage. Consequently, those forest may be accelerating the global carbon cycle, considering that fast-growing pioneer trees have lower wood density rates and sequester less carbon than do the mature-phase trees they usually replace (Laurance et al., 2006).

Nonetheless, the forest resilience ability may strongly depend on the variety of functional groups present, the accumulated resources that supply the recovery and the ecosystem ecological memory (Gunderson, 2000; Ciemer et al., 2019; Hughes et al., 2019), justifying divergences among studies.

In this way, recognize how trees occupying distinct forest vertical profile are being affected and responding to forest fragmentation along their life's cycle may provide more truly insights on the resilience of the Amazonian forest, in face of the current scenario of increasing forest loss, forest fragmentation and climate change. This become relevant since most global forest remnants are less than 10 ha in area, and half of the world's forest is within 500 m of the forest edge (Haddad et al., 2015). Added to that, some estimates suggest that edge areas degradation of tropical forests may account for 9-24% of the total annual carbon loss (Pütz et al., 2014).

Therefore, considering that shallow-rooted small trees (between 20 and 30 cm in diameter at breast height, DBH) can represented 45% of the above-ground biomass in Amazonian forest areas (Vieira et al., 2004). And if Amazonian trees occupying different positions in the forest vertical profile show growth divergence when exposed to edge effects, reflecting in distinct resilience capacity; this study seeks, using a dendrochronological approach, evaluate how *Theobroma sylvestre* Mart. (Malvaceae) trees, typically located at

lower position in the vertical profile of *terra firme* type of Amazonian forest are being affected and respond to forest fragmentation and edge effects along their life's cycle, we address the following questions:

- (i) Are individual growth patterns of trees located close to a forest edge affected compared with trees located far from the edge?
- (ii) If yes, what is the temporal extent of edge effect influence tree growth patterns?
- (iii) Are edge effects boosting growth release events?
- (iv) Trees occupying different position in the forest vertical profile show growth divergence when exposed to edge effects?

Materials and Methods

Study and sampling areas

The present study was carried out in the Biological Dynamics of Forest Fragments Project (BDFFP) study sites, the world's largest and longest-running experimental study of tropical habitat fragmentation (Lovejoy et al., 1986; Laurance et al., 2018). The BDFFP is located 80 km North of Manaus, Brazil (2°30'S, 60°W) and covers an area of ~1000 km². A description of the project and the location of all fragments and control areas can be found in Gascon and Bierregaard (2001). The total annual precipitation ranges from 1900 to 3500 mm with a moderate, but remarkable dry season (<100 mm/month) from June to October (Laurance et al., 2018).

Under a phytophysiology-based definition, the sampled area is typified mature *terra firme* forest, a term used for non-flooded Amazonian forests, which represents 80% of the Biome (Pires and Prance, 1985). In general, four strata define the structure of the forest: understory, sub-canopy, a canopy with a 25-35 m and emergent trees that can reach up to 45 m. An assembly of approximately 1,300 species of trees (>10 cm DBH) represents a forest highly diverse (BDFFP personal communication, 2019).

For the present study, two BDFFP reserves were visited to collect wood samples from trunks of *Theobroma sylvestri* trees (Fig 1). Trees exposed to edge effects were located close to the edge or at most, 300 m far from any edge in the Porto Alegre ranch, specifically at the 100-ha reserve (2°22'2.82" S, 59°58'31.63" W). The reserve was created in August of 1983, by cutting and burning the surrounding pristine forest to establish a new pastureland. We defined the penetration distance of edge effects up to 300 m because increasing tree mortality associated to forest fragmentation can be detectable until this distance (Laurance et al., 2018). Trees not exposed to edge effects were sampled at Esteio ranch, at the continuous forest

located within the Km 41 reserve ($2^{\circ}26'15.52''$ S, $59^{\circ}46'1.25''$ W). Trees were located at least 1000 m far from the nearest edge (a narrow unpaved road). The reserve was created in 1984, and the forest was kept intact, and it is considered one of the control areas.

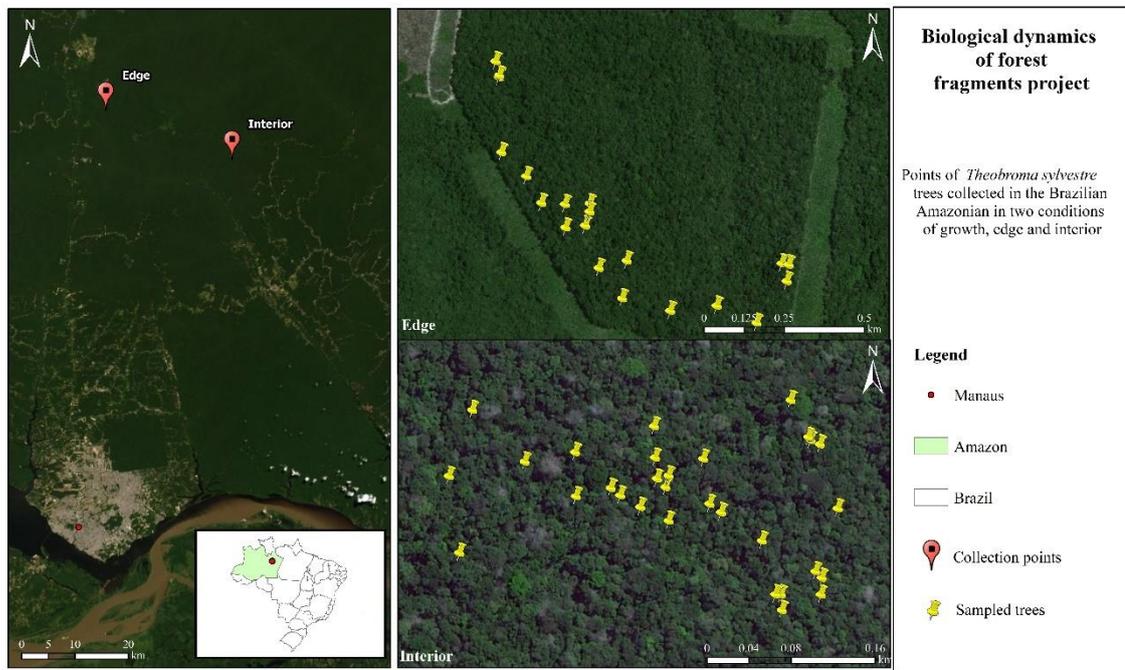


Figure 14. Location (red dots) of the two study sites of *terra firme* forests at the Biological Dynamics of Forest Fragments Project (BDFFP) in Central Amazonia (left). Yellow dots indicate sampled trees in the forest fragment of the Porto Alegre ranch (upper right map) and in continuous forest at the Esteio ranch (lower right map).

Theobroma sylvestri tree-ring analysis

Theobroma is a genus of the Neotropics which its geographical distribution is related to lowland rainforests extending from Southern México to the Amazon Basin (Cuatrecasas, 1964). Commonly known as “cocoa”, *Theobroma sylvestri* reaches an arboreal size not exceeding 18 m in height, conditioning individuals to the lower and intermediate positions of the vertical profile of the Amazonian Forest (Ducke, 1953). Although *Theobroma sylvestri* is not widely used for cocoa butter production, its potential is recognized (Gilabert-Escrivá, Gonçalves, Silva, & Figueira, 2002).

For dendroecological analyzes we took wood samples between April and October 2016 from a total of 50 trees, 20 growing close to the forest edge and 30 into the interior of the continuous forest. The sampled trees were in good phytosanitary condition and did not presented vines. Three radial cores were collected for each tree at DBH using increment borers (diameter = 5.1 mm). Each core was polished with different abrasive sandpaper (from

80 to 600 grains/cm²) with the aim of revealing tree ring boundaries. Subsequently, all tree rings were identified and dated with the help of a stereomicroscope according to the classic method using narrow rings as pointer years (Stokes & Smiles, 1996). After identification, all tree-ring series were scanned at a resolution of 2400 dpi by an HP G4050 scanner. Measurements of tree-ring widths were performed with a precision of 0.001 mm through the software Image J.

To evaluate dating accuracy, the temporal series of ring widths were compared within and among trees at each site. Both visual and statistical cross dating were performed. Visual cross dating was done working with ring-width bar plots, and statistical cross dating was tested using COFECHA software (Holmes, 1983). COFECHA uses segmented temporal series correlation techniques to assess the quality of cross dating and measurement accuracy in the tree ring time series (Grissino-Mayer, 2001).

After evaluating the dating in COFECHA software, we sought to construct master chronologies for each site that would increase the retention of common growth signals. According to Cook and Kairiukstis (1990), spline functions with length between 67 and 75% of the series are able to remove biological growth trends related to high frequency variances. To build up site chronologies, time series were detrended and standardized using a smoothed cubic spline function with 50% frequency-response cut-off for 65% of the length of each series in dplR package in R Software (A. G. Bunn, 2008). The standardization of the series was performed by dividing the width of the tree ring by the growth model of the smooth cubic spline function, producing dimensionless ring-width indices (RW) (A. Bunn & Korpela, 2017). The quality of the chronology was evaluated by the value of Rbar and EPS (expressed population signal), both calculated with the dplR package on R Software (Bunn, 2008). The Rbar is the average correlation coefficient resulting from comparing all possible segments of a predetermined length among all the series included in the chronology (Briffa, 1995). The EPS values provided information that confirmed the existence of common signals among trees, EPS values higher than 0.80 indicate that the limiting factor of growth in the chronology probably is homogenous (Mendivelso, Camarero, Gutiérrez, & Zuidema, 2014).

Site growth patterns

To explore the growth patterns among trees located close to the edges and trees located into the interior of the forest, the width of the tree rings was converted into basal area increment (BAI). BAI is considered a more informative measure of tree growth trends in terms of total biomass production (Peñuelas, Canadell, & Ogaya, 2011; Phipps & Whiton,

1988). The width of the tree rings was converted to BAI according to the following standard formula: $BAI = \pi (R_{2n} - R_{2n-1})$, where R is the tree radius and n is the tree ring formation year. To calculate BAI we used the `bai.out` function in `dplR` package in software R (A. G. Bunn, 2008; A. Bunn & Korpela, 2017).

Principal Component Analysis (PCA) was performed to identify dominant BAI patterns between edge and interior trees during common growth periods: all periods (1970 to 2015), before edge creation (1970 to 1982), five years after forest fragmentation (1983 to 1987), ten years after forest fragmentation (1983 to 1992), fifteen years after forest fragmentation (1983 to 1997), twenty years after forest fragmentation (1983 to 2002), twenty five years after forest fragmentation (1983 to 2007), and at last, thirty years after forest fragmentation (1983 to 2012).

The PCA was realized by the `prcomp` function in R software (R core Team, 2017). Through the data dimension reduction, the PCA automatically performs data clustering according to the K-means objective function (Ding & He, 2004). Thus, seeking cluster validation of trees exposed and unexposed to edge effects, Silhouette Index (SI) (Rousseeuw, 1987) was used. The SI evaluates how much a sample is similar to another inserted in the same cluster, comparing with samples inserted in other clusters (Kaufman & Rousseeuw, 2009). SI values near +1 indicate that the sample is far from the neighboring clusters, confirming that the sample was correctly allocated. A value of 0 indicates that the sample is very close to the decision boundary between two neighboring clusters, and negative values indicate that sample might have been assigned to the wrong cluster (Rousseeuw, 1987). After PCA, we used Kruskal-Wallis test ($p < 0.05$) to compare BAI trends between edge and interior clusters.

Disturbance analysis

Some of the most widely used methods for identifying release events are radial growth averaging techniques, in which a growth change percentage (%GC) calculation is made on each tree-ring time series, and release events are recorded when growth change percent values exceed a certain minimum value (Nowacki and Abrams, 1997; Black et al., 2009;). In this way, to detect release events we used the formula of Nowacki and Abrams (1997) to derive the growth change percentages: $\%GC = [(M2 - M1) / M1] \times 100$, where %GC = growth change percentage for year 1, $M1$ = mean diameter growth over the preceding 10 years, and $M2$ = mean diameter growth over the subsequent 10 years. Studies in tropical forests reveal that a moving average of 10 years was able to remove long-term age-effects and short-term

climatic fluctuations (Brienen and Zuidema, 2006; Brienen et al., 2010). Release events were identified when the %GC was greater than 50% during a minimum period of 10 years (Rozendaal, Soliz-Gamboa, & Zuidema, 2011). Release events were performed by overall function by the Nowacki and Abrams (1997) method using the “TRADER” package (Altman, Fibich, Dolezal, & Aakala, 2014) in R (R core Team, 2017).

Seeking to verify if the %GC that promoted release events before and after the edge creation induced statistically significant differences in the wood production, Kruskal-Wallis test ($p < 0.05$) was performed on the growth changes of BAI (Δ BAI). Δ BAI was calculated as the difference in the BAI average ten years before the release events and ten years after the release events.

Results

Tree-ring chronologies of *Theobroma sylvestre*

The tree rings of *Theobroma sylvestre* in edge and interior sites were distinct and characterized by growth layers demarcated by the flattening of the fibers and tangentially distended rays (Fig 15).

The master chronology (Fig 16) was built from tree-ring widths covering a period of 69 years (1947-2015) for trees located close to the edge and 57 years (1959-2015) for trees located at the interior of the forest, confirming the presence of the trees before forest fragmentation and edge creation in 1983. The cross-dating quality and accuracy in the measurements of the tree rings was confirmed by the correlations, $EPS > 0.80$ and $Rbar > 0.3$ values, indicating a common growth pattern in edge and interior study sites. The descriptive statistics of the chronologies are presented in Table 6.

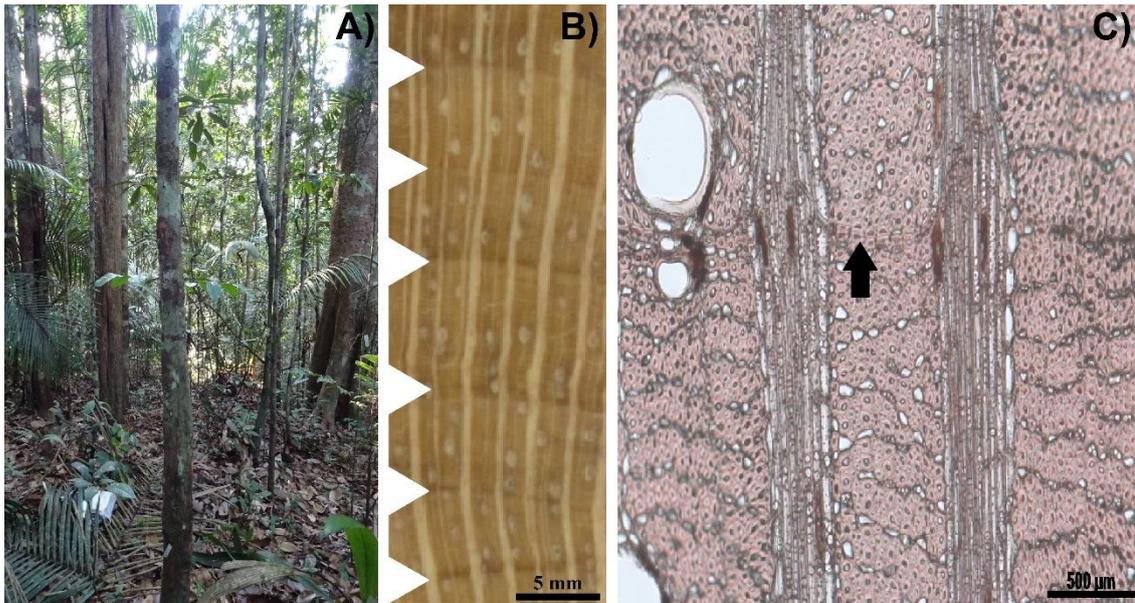


Figure 15. A) *Theobroma sylvestre* tree in the edge of the reserve at the Biological Dynamics of Forest Fragments Project site; B) Macro and C) Microscopic images of the transverse wood section evidencing the tree ring anatomy characterized by growth layers demarcated by the flattening of the fibers and tangentially distended rays. White triangles indicate the growth-rings limits and black arrows indicate the fiber flattening.

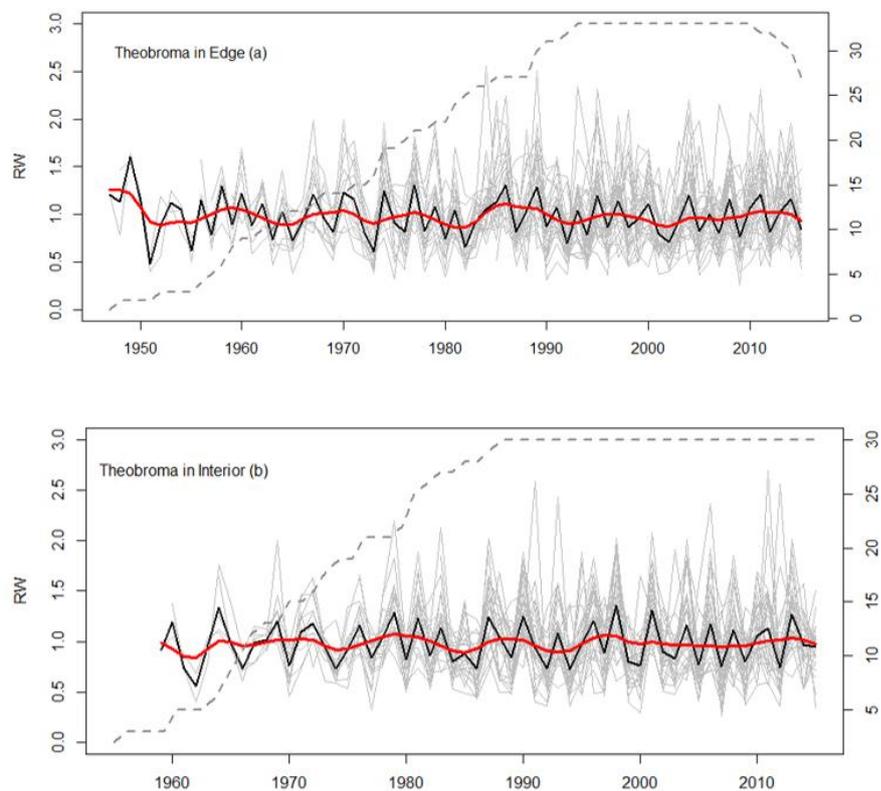


Figure 16. Residual tree-ring chronology of *Theobroma sylvestre* trees for Edge (a) and Interior (b) locations in *terra firme* type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. Grey solid line: individual average time series; black line: residual tree-ring master chronology; grey dotted line: number of radial cores used for the index calculation; red line: standardization of master chronology by a 10% smoothed spline curve.

Table 6. Descriptive statistics of the chronologies of *Theobroma sylvestre* trees located close to the edge and in the interior of the forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.

Variables	Edge	Interior
No. trees/No. radial cores	17/33	19/30
Mean ring width \pm SD (cm)	0.08/0.02	0.08/0.04
Time span	1947- 2015	1959-2015
Age \pm s	50/11	43/8
Mean sensitivity	0.36	0.39
Series intercorrelation	0.50	0.51
Rbar (\pm SD)	0.32/0.03	0.31/0.02
Period with EPS \geq 0.80	1955-2015	1965-2015

Site growth patterns

After the construction of the chronologies and the growth-ring annuity confirmation, we sought to compare edge and interior population growth patterns with similar age and diameter structure, seeking to avoid ontogenetic influences. For this, 13 trees located close to the edge and 11 trees located in the interior of the forest representing populations of similar ages and diameter classes, corresponding a common growth period (1970–2015) were selected (Table 7).

Table 7. Age and diameter at breast height (DBH) of *Theobroma sylvestre* trees at edge and interior sites in *terra firme* type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia selected for growth pattern analyzes.

Year	Edge		Interior	
	DBH	Age	DBH	Age
1970	1.09 (SD \pm 0.7)	10 (SD \pm =4)	1.02 (SD \pm =0.7)	7 (SD \pm 5)
1982	2.53 (SD \pm 1.4)	16 (SD \pm =9)	2.52 (SD \pm 1.5)	15 (SD \pm 7)
2015	8.03 (SD \pm 1.4)	49 (SD \pm =9)	7.05 (SD \pm 2.7)	48 (SD \pm 7)

Results, as evidenced in Fig 5 and Table 3, revealed a temporal influence of edge effects on the BAI rate dynamics of *Theobroma sylvestre* trees. Thus, during the whole study period (1970 to 2015), before the forest fragmentation (1970 to 1982), twenty five years after forest fragmentation (1983 to 2007) and thirty years after forest fragmentation (1983 to 2012), *Theobroma sylvestre* trees exposed (for those trees close to the edge after 1983) and not exposed to edge effects did not present divergent basal area increment rates through the principal component analyzes (Fig 17), which was confirmed by the non-validation of the clusters grouped by the Silhouet index (SI) as well as by absence of statistically significant differences through the Kruskal-Wallis test ($p > 0.05$; Table 8).

However, influences associated to the formation of edges effects were identified during the next 10 years (1983 to 1992), 15 years (1983 to 1997) and also 20 years (1983 to 2002) after forest fragmentation, periods when trees near to the edge showed increases of 11%, 10 % and 6%, respectively in BAI rates compared to trees not exposed to edge effects. The results were validated by the PCA analysis (Fig 4), Silhouette index (> 0.6), and non-parametric ANOVA (Table 8), proving the temporality of the edge effects on the growth dynamics of the trees. Through the analysis of ordination, we found that BAI divergences among populations during these three periods (10, 15 and 20 years after forest fragmentation) were retained mainly by component two, responsible for approximately 11% of the data variance. It is also possible to observe a more similar growth behavior retained by component one, responsible for approximately 66% of the data variance; however, this ordering did not present enough strength to join the clusters of the two populations in component one. That is, during these three periods, the ordination of the edge and interior trees cluster was favored by a signal of lower intensity, retained by component two of the PCA and related to edge effects.

During the first five years after forest fragmentation (1983 to 1987), divergences in BAI rates among populations are evidenced from the PCA analysis, mainly through component two, responsible for the retention of 18% of the data variance and ordination of the edge and interior trees clusters, validated by the index of Silhouette (> 0.7). Nevertheless, although the ordination of trees in edge and interior clusters by PCA, this divergence in BAI rates during the first five years of forest fragmentation was not confirmed by non-parametric Kruskal-Wallis ANOVA ($p > 0.05$). In this sense, we believe that the strength of the most common sign of growth between populations, observed through component one of the PCA, responsible for 72% of the data variance, exerted a greater influence on the BAI dynamics of the trees, reflecting the absence of differences in the five years after forest fragmentation through frequentist inference.

Disturbance analysis

In general, during the evaluated period of 45 years, 11 growth release events were observed in trees located close to the edge, but these events were observed only after the forest fragmentation and edge creation. Most release events in trees exposed to edge effects were observed during the first five years after forest fragmentation, where 25% of the trees presented growth release. Trees in the interior of the forest, presented seven growth release events during the same 45 years evaluated (Fig 17), also there were detected mainly after

1983. However, contrary to the trees exposed to edge effects, most of these events have been observed after the first five years after forest fragmentation.

Non-parametric analysis confirmed that the BAI growth changes (Δ BAI) of trees close to the edge after forest fragmentation (1983 to 2015) (Δ BAI = 1.09 cm²; SD \pm 0.22) was, on average 50% higher than those occurred in trees distant do the edge (Δ BAI = 0.47 cm², SD \pm 0.13) during the same period. That is, release events after forest fragmentation induced higher growths in trees exposed to edge effects compared to trees in control areas.

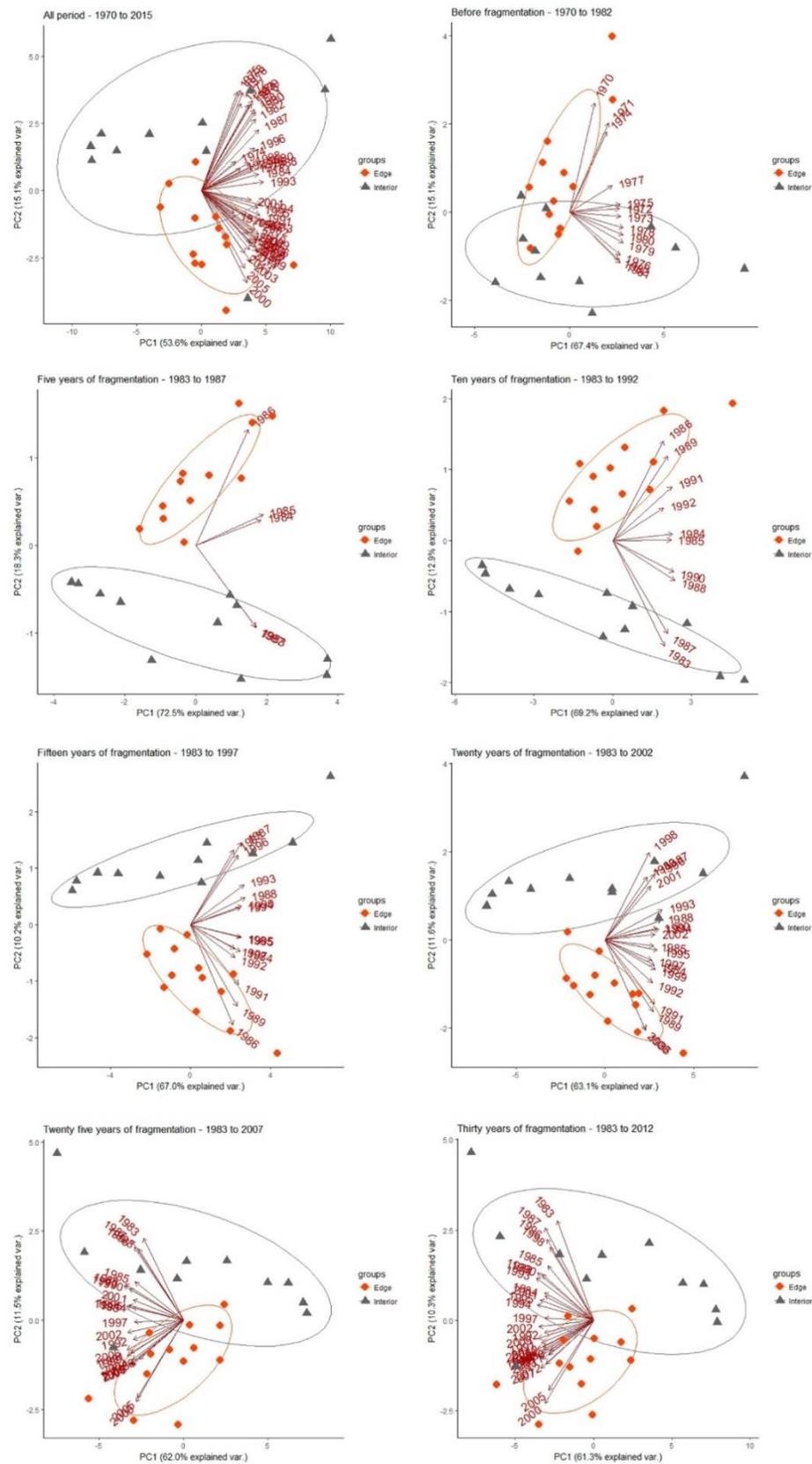


Figure 17. Principal Component Analysis described by BAI series of *Theobroma sylvestre* trees located close to the edge (orange circles) and into the interior of the forest (gray triangles) in *terra firme* type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.

Table 8. Basal area increments (BAI) of *Theobroma sylvestri* trees located close to the edge (Edge BAI) and in the interior of the forest (Interior BAI) during a common growth time period in *terra firme* forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. The asterisks indicate the statistically significant differences by Kruskal-Wallis test ($p < 0.05$).

	BAI Edge	BAI Interior
1970 to 2015 – entire period	0.98 cm ² , s=0.78	0.83 cm ² , s=0.84
1970 to 1982 – before forest fragmentation	0.20 cm ² , s=0.15	0.28 cm ² , s=0.32
1983 to 1987 – 5 yrs after forest fragmentation	0.61 cm ² , s=0.24	0.60 cm ² , s=0.48
1983 to 1992 – 10 yrs after forest fragmentation	0.77 cm², s=0.30 *	0.68 cm², s=0.50 *
1983 to 1997 – 15 yrs after forest fragmentation	0.86 cm², s=0.39 *	0.78 cm², s=0.64 *
1983 to 2002 – 20 yrs after forest fragmentation	0.94 cm², s=0.42 *	0.88 cm², s=0.70 *
1983 to 2007 – 25 yrs after forest fragmentation	1.0 cm ² , s=0.52	0.93 cm ² , s=0.75
1983 to 2012 – 30 yrs after forest fragmentation	1.21 cm ² , s=0.65	1.00 cm ² , s=0.87

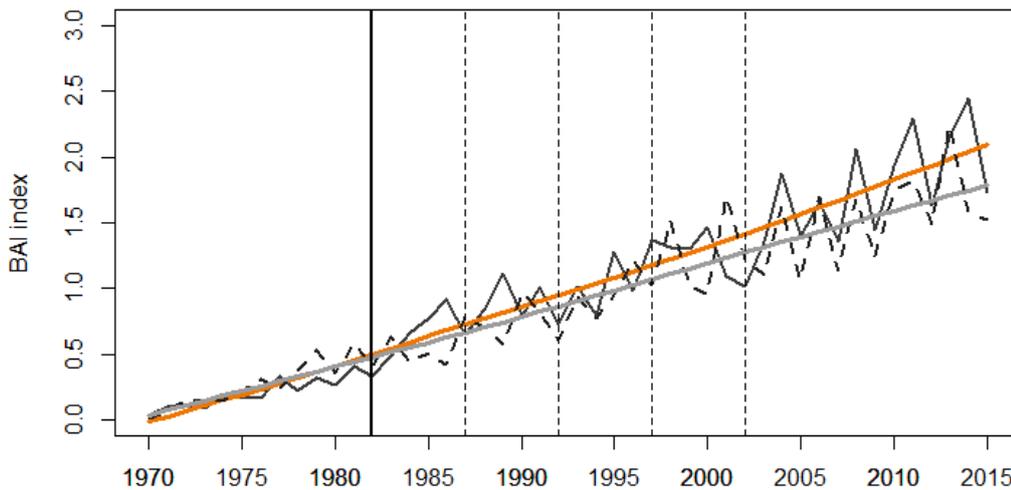


Figure 18. Dominant basal area increment (BAI) index patterns of *Theobroma sylvestri* trees located close to the edge (solid black lines) and in the interior of the forest (dashed black line) in *terra firme* forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. Orange line: standardization by a 30% smoothed spline curve of BAI chronology of trees located close to the edge; gray line: standardization by a 30% smoothed spline curve of BAI chronology of trees in the interior of the forest; vertical solid black line: edge creation year (1982); vertical dashed black line: five, ten, fifteen and twenty years after edge creation.

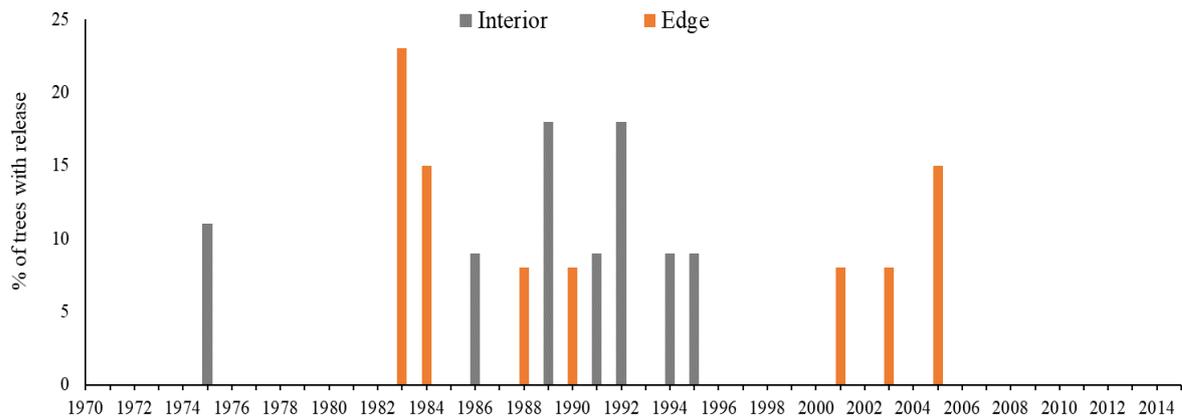


Figure 19. Release events in *Theobroma sylvestre* trees close to the forest edge (orange) and into the interior of the forest or far from the edge (gray) in *terra firme* type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia.

Discussion

When we registered the edge effects temporality on *Theobroma sylvestre* trees growth dynamics, we may attribute this phenomenon to the Amazonian rainforest resilience after forest fragmentation. This resilience capacity strengthens the fundamental role of the Amazonian forest in maintenance and conservation of processes essential to human well-being, which can be recognized through ecosystem services, depending on how people value nature (Fearnside, 1997; Thompson & Barton, 1994).

Considering that tropical forests with an extensive history of disturbance and human occupation such as the Brazilian Atlantic rainforest (Dean, 1996), are losing this resilience capacity, not presenting differences between carbon stock, basal area or tree stem density between edge and forest interior sites (d'Albertas et al., 2018). We highlight the role of trees that survived after forest fragmentation and edge creation process, as bioindicators of Amazonian rainforest conservation status, revealing in the absence of structural divergences with trees in the interior of the forest, the criticality of the environmental problem.

Newly created forest edges are structurally more open and permeable to penetration of light and hot dry winds from the adjacent anthropic matrix (e.g. pasture or agricultural crops) (Camargo & Kapos, 1995; Murcia, 1995), making the gradient of edge and interior of the forest very intense, especially in the first five years after forest fragmentation (Laurance et al., 2002). In this sense, by potentiating the solar radiation penetration in the understory, exceeding the 3% that reaching the soil of the non-fragmented Amazonian forest (Shuttleworth et al., 1984), we could expect that immediately after edge creation, trees in the

understory would be favored by increased radiation, consequently presenting releases in the growth rate (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006).

Remote sensing techniques confirmed the Amazonian understory trees density increased in response to canopy variation and opening (Tang & Dubayah, 2017), corroborating with recent studies that considered the canopy phenology an essential influence of photosynthetic seasonality in Amazonian forest (Wu et al., 2016, 2018).

In BDFFP areas, changes in canopy structure after five years of forest fragmentation also favored the understory vegetation density increase (Camargo & Kapos, 1995). Although, after 22 years of forest fragmentation, the increase regeneration of pioneer trees favored the canopy reorganization, reflecting the greatest leaf area index in the midstory (5-25 m) (Almeida et al., 2019).

Trees located in lower forest structural positions, span broad functional spectrum, ranging from light demanding to shade tolerant plants (Wright et al., 2010). *Teobroma sylvestre* trees belongs to the functional group of shade tolerant species (Ribeiro et al., 1999), plants capable of germinating under closed canopies, although presenting development and reproduction accentuated by the increase of light incidence in clearings (Whitmore, 1989).

However, even though the first five years after forest fragmentation are considered the most intense period in terms of light incidence (Laurance et al., 2002), the absence of statistically significant divergences between the BAI rates of *T. sylvestre* trees exposed and not exposed to edge effects as expressed by the tree ring development, may reveal that the increases in light availability is not benefiting immediately the basal area increment of this trees in lower and intermediate positions of forest vertical profiles, since differences were only proven from the 5th year after forest fragmentation.

This time lag in the expected BAI increase suggests that during the first years of forest fragmentation and edge creation, some understory trees species would be investing more energy in their own basal maintenance or in primary growth in expanding crown and leaf area, favored by canopy opening (Smith et al., 2019). On the other hand, abiotic factors such as temperature increase and humidity reduction, producing a more dramatic dryer environment along the edges were responsible for large structural changes in edge areas (Chen et al., 1999), such conditions could also mitigate the expected BAI increase during the early years of fragmentation. Moreover, the strong competition with fast growing, light-demanding species that proliferate rapidly in fragmented forests (Mantovani, & Peres, 1999; Laurance et al., 2006; Mesquita et al., 2015) can also be influencing the absence of the BAI rates increase.

Results of disturbance analyzes revealed that 25% of the *T. sylvestre* trees exposed to edge effects presented growth release events during the first five years of forest fragmentation. In this sense, we can consider that although the canopy opening promoted increases in the BAI rates of these individuals, these events were not enough to promote statistically significant divergences between trees exposed and not exposed to edge effects during these first years.

Corroborating with these justifications, trees exposed to edge effects presented statistically significant BAI rates increases only during 10, 15 and 20 years after forest fragmentation. This confirms that the microclimate stabilization in edge areas (e.g temperature, humidity and winds) through the establishment of a secondary re-growth vegetation (> 5 years of isolation) (Laurance et al., 2002), would favor the growth of *T. sylvestre* trees located in lower and intermediate forest vertical profile. Since, in more shade environments, slow-growing and shade-tolerant tree species present competitive advantages over fast growing, light-demanding trees (Grime & Pierce, 2012; Mesquita et al., 2015).

After 20th year of fragmentation, the Amazonian forest edge resilience have already driven the return to microclimatic and phytophysiognomic similarities in relation to areas distant from the edge. Reflecting the divergence absence in BAI rates among *T. sylvestre* trees exposed and not exposed to edge effects. Corroborating with the observed results through *T. sylvestre* tree rings, Almeida et al. (2019) did not found in the same study areas of BDFFP, basal area and above ground biomass (AGB) divergences related to edge distance after 22 years of forest fragmentation. Thus, we can consider that edge areas could enhance the growth of some species in lower canopy positions mainly during the first 20 years of fragmentation.

It is interesting to compare these results with those observed for *Scleronema micranthum* (Ducke) Ducke, a typical canopy trees present in the edges and interior forest of the BDFFP areas. In opposition of understory trees, those trees exhibited, during the first five and 10 years after forest fragmentation and edge creation, BAI rates reduction by around 20% and 16%, respectively (Albiero-Júnior et al., 2019).

Taller and large trees occupying the forest canopy, are more vulnerable to drought stress, needing to deal with higher vapor pressure deficit (VPD), higher light interception and hydraulic path length (McDowell and Allen, 2015; Longo et al., 2018). Being generally more vulnerable to xylem embolism, this species operates with small safety margins (Brum et al., 2019). Rain exclusion studies conducted in Eastern Amazon, confirmed that hydraulic failures may be the main cause of increased mortality of large trees (Nepstad et al., 2007; Rowland et al., 2015; Meir et al., 2015). On the other hand, understory trees are exposed to lower VPD,

and are able to tolerate or do not experience the same levels of drought stress (Smith et al., 2019), because were directly or indirectly protected by canopy's shade, and also presenting greater xylem resistance to embolism formation (Brum et al., 2019).

In this way, it is believed that the microclimatic changes, such as elevated temperatures, reduced humidity and increased vapor pressure deficits occurring in newly created edges lead to depleted soil moisture, creating drought stress (Camargo and Kapos, 1995; Malcolm, 1998; Sizer and Tanner, 1999; Pinto et al., 2010) and exerting more strong pressure on the growth dynamics of emergent and canopy trees. However, the canopy losses can potentiate light availability at the understory, favoring small trees to growth and proliferate (Longo et al., 2018).

Many studies have confirmed that after forest fragmentation, the proliferation of pioneers trees became an important component of above ground biomass stocks recover (Bierregaard Jr et al., 1992; Ferreira and Laurance, 1997; Nascimento and Laurance, 2004; Laurance et al., 2006; Shimamoto et al., 2014; Almeida et al., 2019). However, fast-growing pioneer trees have lower wood density, consequently sequester less carbon and have less longevity, reducing the carbon stock time in trees (Nascimento and Laurance, 2004; Laurance et al., 2006). That is, Amazonian forest fragmentation may reduce above-ground biomass stocks of the largest terrestrial carbon sink (Brienen et al., 2015).

In this sense, our study using dendrochronological approach could suggest that the increase in basal area increment rates of trees in lower and intermediate forest vertical profile, may reveal an important component of above ground biomass stocks recover, after forest fragmentation, mainly during the first 20 years of edge creation. A fact that should be considering in forest management and restoration practices. Promoting new perspectives to forest resilience ability after fragmentation processes.

Conclusion

Our dendrochronological study revealed that edge areas are favoring the growth of *Theobroma sylvestre* trees, a typical species located in lower and intermediate forest vertical profile of terra firme Amazonian forest, mainly during the first 20 years after forest fragmentation and edge creation. At the same time, an opposite behavior was found for canopy trees, as registered to *Scleronema micranthum*, especially during the first 10 years and the same type of edge (Albiero-Júnior et al., 2019). Indicating that the microclimatic and structural changes induced by edge effects exert contrasting influences on tree growth, according to the different positions they occupy in the Amazonian forest vertical profile. In

addition, we highlight that the increase in basal area increment for those trees in lower and intermediate forest vertical profile exposed to edge effects, may indicate an important role in above ground biomass stocks recover, after forest fragmentation, a fact that should be considered in forest management and restoration practices. Promoting new perspectives to forest resilience ability after fragmentation processes. However, we also highlight the need to extend the study to a larger number of species, to confirm these hypotheses.

Acknowledgements

This work was funded by the Rufford Small Grant for Nature Conservation (<http://www.rufford.org/>, RSGA application 18762-1), BDFFP Thomas Lovejoy research fellowship program and conducted during a scholarship supported by the International Cooperation Program CAPES/PVE (process: 88887.127558/2016-00) at Laboratorio de Dendrocronología y Ciencias Ambientales from the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA-CONICET), Mendoza, Argentina. The first author was supported by a PhD scholarship from CAPES – Brazilian Federal Agency for the Improvement of Higher Education Personnel. This is the number XXX publication of the Biological Dynamics of Forest Fragment Project (BDFFP – INPA/STRI) Technical Series.

References

- Albiero-Júnior, A., Venegas-González, A., Botosso, P. C., Roig, F. A., Camargo, J. L. C., & Tomazello-Filho, M. (2019). What is the temporal extension of edge effects on tree growth dynamics? A dendrochronological approach model using *Scleronema micranthum* (Ducke) Ducke trees of a fragmented forest in the Central Amazon. *Ecological Indicators*, 101, 133–142.
- Almeida, D. R. A., Stark, S. C., Schiatti, J., Camargo, J. L. C., Amazonas, N. T., Gorgens, E. B., ... Saleska, S. (2019). Persistent effects of fragmentation on tropical rainforest canopy structure after 20 years of isolation. *Ecological Applications*, 29, 1221-1235.
- Altman, J., Fibich, P., Dolezal, J., & Aakala, T. (2014). TRADER: a package for tree ring analysis of disturbance events in R. *Dendrochronologia*, 32, 107–112.
- Baker, P. J., & Bunyavejchewin, S. (2006). Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. *Journal of Tropical Ecology*, 22, 521–529.

- Berenguer, E., Gardner, T. A., Ferreira, J., Aragão, L. E. O. C., Mac Nally, R., Thomson, J. R., ... Barlow, J. (2018). Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. *Journal of Ecology*, 106, 2190–2203.
- Bierregaard Jr, R. O., Lovejoy, T. E., Kapos, V., dos Santos, A. A., & Hutchings, R. W. (1992). The biological dynamics of tropical rainforest fragments. *BioScience*, 42, 859–866.
- Black, B. A., Abrams, M. D., Rentch, J. S., & Gould, P. J. (2009). Properties of boundary-line release criteria in North American tree species. *Annals of Forest Science*, 66, 205–206.
- Brienen, R J W, Zuidema, P. A., & Martinez-Ramos, M. (2010). Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions. *Oecologia*, 163, 485–496.
- Brienen, Roel J W, Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., Lewis, S. L. (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–348.
- Brienen, Roel J W, & Zuidema, P. A. (2006). Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *Journal of Ecology*, 94, 481–493.
- Briffa, K. R. (1995). Interpreting high-resolution proxy climate data—the example of dendroclimatology. In *Analysis of Climate Variability* (pp. 77–94). Springer.
- Brum, M., Vadeboncoeur, M. A., Ivanov, V., Asbjornsen, H., Saleska, S., Alves, L. F., Barros, F. (2019). Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *Journal of Ecology*, 107, 318–333.
- Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, 26, 115–124.
- Bunn, A., & Korpela, M. (2017). An introduction to dplR.
- Callede, J., Cochonneau, G., Vieira Alves, F., Guyot, J.-L., Santos Guimaraes, V., & De Oliveira, E. (2010). The river amazon water contribution to the atlantic Ocean. *Revue Des Sciences de l'eau*, 23, 247–273.
- Camargo, J. L. C., & Kapos, V. (1995). Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*, 11, 205–221.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., ... Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, 49, 288–297.

- Cierner, C., Boers, N., Hirota, M., Kurths, J., Müller-Hansen, F., Oliveira, R. S., & Winkelmann, R. (2019). Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall. *Nature Geoscience*, 12, 174.
- Cook, E. R., & Kairiukstis, L. A. (1990). *Methods of dendrochronology: applications in the environmental sciences*. Amsterdam: Kluwer.
- Cuatrecasas, J. (1964). *Cacao and its allies; a taxonomic revision of the genus Theobroma*.
- d'Albertas, F., Costa, K., Romitelli, I., Barbosa, J. M., Vieira, S. A., & Metzger, J. P. (2018). Lack of evidence of edge age and additive edge effects on carbon stocks in a tropical forest. *Forest Ecology and Management*, 407, 57–65.
- de Paula, M. D., Groeneveld, J., & Huth, A. (2016). The extent of edge effects in fragmented landscapes: Insights from satellite measurements of tree cover. *Ecological Indicators*, 69, 196–204.
- Dean, W. (1996). *A ferro e fogo: a história e a devastação da Mata Atlântica brasileira*. Companhia das Letras.
- Ding, C., & He, X. (2004). K-means clustering via principal component analysis. *Proceedings of the Twenty-First International Conference on Machine Learning*, 29. ACM.
- Ducke, A. (1953). *As espécies brasileiras do gênero Theobroma L. (Boletim técnico do instituto agrônômico do norte, ed.)*. Belém.
- Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo, A., Brienen, R. J. W., Ter Steege, H. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, 6, 7857-7866.
- Fearnside, P. M. (1997). Environmental services as a strategy for sustainable development in rural Amazonia. *Ecological Economics*, 20, 53–70.
- Ferreira, L. V, & Laurance, W. F. (1997). Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conservation Biology*, 11, 797–801.
- Freitas, F. L. M., Sparovek, G., Berndes, G., Persson, U. M., Englund, O., Barretto, A., & Mörtberg, U. (2018). Potential increase of legal deforestation in Brazilian Amazon after Forest Act revision. *Nature Sustainability*, 1, 665-670.
- Gascon, C., & Bierregaard Jr, R. O. (2001). The biological dynamics of forest fragments project. *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*, 31–42.

- Gilabert-Escrivá, M. V., Gonçalves, L. A. G., Silva, C. R. S., & Figueira, A. (2002). Fatty acid and triacylglycerol composition and thermal behaviour of fats from seeds of Brazilian Amazonian *Theobroma* species. *Journal of the Science of Food and Agriculture*, 82, 1425–1431.
- Grime, J. P., & Pierce, S. (2012). *The evolutionary strategies that shape ecosystems*. John Wiley & Sons.
- Grissino-Mayer, H. D. (2001). Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. *Tree-Ring Research*, 57, 205–221.
- Gunderson, L. H. (2000). Ecological resilience—in theory and application. *Annual Review of Ecology and Systematics*, 31, 425–439.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Collins, C. D. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, 1-9.
- Hilker, T., Lyapustin, A. I., Tucker, C. J., Hall, F. G., Myneni, R. B., Wang, Y., ... Sellers, P. J. (2014). Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings of the National Academy of Sciences*, 111, 16041–16046.
- Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43, 69–78.
- Hughes, T. P., Kerry, J. T., Connolly, S. R., Baird, A. H., Eakin, C. M., Heron, S. F., ... Liu, G. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change*, 9, 40-43.
- INPE. (2019). Satellite-based monitoring of deforestation of the Amazon forest/PRODES “Monitoramento da floresta amazônica brasileira por satélite”.
- Kaufman, L., & Rousseeuw, P. J. (2009). *Finding groups in data: an introduction to cluster analysis* (Vol. 344). John Wiley & Sons.
- Laurance, W. F., Camargo, J. L. C., Fearnside, P. M., Lovejoy, T. E., Williamson, G. B., Mesquita, R. C. G., ... Laurance, S. G. W. (2018). An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*, 93, 223–247.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C. Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, 16, 605–618.
- Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E. L., & Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, 87, 469–482.

- Letcher, S. G., & Chazdon, R. L. (2009). Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, 41, 608–617.
- Longo, M., Knox, R. G., Levine, N. M., Alves, L. F., Bonal, D., Camargo, P. B., ... Saleska, S. R. (2018). Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts. *New Phytologist*, 219, 914–931.
- Lovejoy, T. E., Bierregaard Jr, R. O., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., ... Schubart, H. O. R. (1986). Edge and other effects of isolation on Amazon forest fragments.
- Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., ... Becker, K. M. L. (2018). Global importance of large-diameter trees. *Global Ecology and Biogeography*, 27, 849–864.
- Malcolm, J. R. (1998). A model of conductive heat flow in forest edges and fragmented landscapes. *Climatic Change*, 39, 487–502.
- Malhi, Y., Wood, D., Baker, T. R., Wright, J., Phillips, O. L., Cochrane, T., ... Arroyo, L. (2006). The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, 12, 1107–1138.
- McDowell, N. G., & Allen, C. D. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, 5, 669.
- Meir, P., Wood, T. E., Galbraith, D. R., Brando, P. M., Da Costa, A. C. L., Rowland, L., & Ferreira, L. V. (2015). Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: insights from field experiments. *BioScience*, 65, 882–892.
- Mendivelso, H. A., Camarero, J. J., Gutiérrez, E., & Zuidema, P. A. (2014). Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity. *Agricultural and Forest Meteorology*, 188, 13–23.
- Mesquita, R. de C. G., Massoca, P. E. dos S., Jakovac, C. C., Bentos, T. V., & Williamson, G. B. (2015). Amazon rain forest succession: Stochasticity or land-use legacy? *BioScience*, 65, 849–861.
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, 10, 58–62.
- Nascimento, H. E. M., & Laurance, W. F. (2004). Biomass dynamics in Amazonian forest fragments. *Ecological Applications*, 14, 127–138.

- Nepstad, D. C., Tohver, I. M., Ray, D., Moutinho, P., & Cardinot, G. (2007). Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, 88(9), 2259–2269.
- Nowacki, G. J., & Abrams, M. D. (1997). Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, 67, 225–249.
- Peñuelas, J., Canadell, J. G., & Ogaya, R. (2011). Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography*, 20, 597–608.
- Phipps, R. L., & Whiton, J. C. (1988). Decline in long-term growth trends of white oak. *Canadian Journal of Forest Research*, 18, 24–32.
- Pinto, S. R. R., Mendes, G., Santos, A. M. M., Dantas, M., Tabarelli, M., & Melo, F. P. L. (2010). Landscape attributes drive complex spatial microclimate configuration of Brazilian Atlantic forest fragments. *Tropical Conservation Science*, 3, 389–402.
- Poorter, L., Bongers, F., Aide, T. M., Zambrano, A. M. A., Balvanera, P., Becknell, J. M., ... Chazdon, R. L. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, 530, 211–214.
- Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A. C., Metz, M., ... Huth, A. (2014). Long-term carbon loss in fragmented Neotropical forests. *Nature Communications*, 5, 5037.
- R core Team, R. (2017). R language definition. Vienna, Austria: R Foundation for Statistical Computing.
- Rangel Pinagé, E., Keller, M., Duffy, P., Longo, M., Dos-Santos, M. N., & Morton, D. C. (2019). Long-Term Impacts of Selective Logging on Amazon Forest Dynamics from Multi-Temporal Airborne LiDAR. *Remote Sensing*, 11, 709.
- Ribeiro, J. E. L. da S., Hopkins, M. J. G., Vicentini, A., Sothers, C. A., Costa, M. A. da S., Brito, J. M. de, Assunção, P. (1999). Flora da reserva ducke. INPA; DFID.
- Rousseeuw, P. J. (1987). Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53–65.
- Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., ... Vasconcelos, S. S. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, 528, 119-122.

- Rozendaal, D. M. A., Soliz-Gamboa, C. C., & Zuidema, P. A. (2011). Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis. *Trees*, 25, 115–124.
- Saatchi, S. S., Houghton, R. A., Dos Santos Alvala, R. C., Soares, J. V., & Yu, Y. (2007). Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology*, 13, 816–837.
- Scarano, F. R., & Ceotto, P. (2015). Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. *Biodiversity and Conservation*, 24, 2319–2331.
- Shimamoto, C. Y., Botosso, P. C., & Marques, M. C. M. (2014). How much carbon is sequestered during the restoration of tropical forests? Estimates from tree species in the Brazilian Atlantic forest. *Forest Ecology and Management*, 329, 1–9.
- Shuttleworth, W. J., Gash, J. H. C., Lloyd, C. R., Moore, C. J., Roberts, J., Marques Filho, A. D. O., Molion, L. C. B. (1984). Eddy correlation measurements of energy partition for Amazonian forest. *Quarterly Journal of the Royal Meteorological Society*, 110, 1143–1162.
- Sizer, N., & Tanner, E. V. J. (1999). Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation*, 91, 135–142.
- Smith, M. N., Stark, S. C., Taylor, T. C., Ferreira, M. L., de Oliveira, E., Restrepo-Coupe, N., ... Alves, L. F. (2019). Seasonal and drought-related changes in leaf area profiles depend on height and light environment in an Amazon forest. *New Phytologist*, 222, 1284–1297.
- Stokes, M. A., & Smiles, T. (1996). *An introduction to tree-ring dating*. Tucson: University of Arizona Press.
- Tabarelli, M, Lopes, A. V, & Peres, C. A. (2008). Edge-effects Drive Tropical Forest Fragments Towards an Early-Successional System. *Biotropica*, 40, 657–661.
- Tabarelli, Marcelo, Mantovani, W., & Peres, C. A. (1999). Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation*, 91, 119–127.
- Tang, H., & Dubayah, R. (2017). Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure. *Proceedings of the National Academy of Sciences*, 114, 2640–2644.
- Teixeira, F. Z., Bachi, L., Blanco, J., Zimmermann, I., Welle, I., & Carvalho-Ribeiro, S. M. (2019). Perceived ecosystem services (ES) and ecosystem disservices (EDS) from trees: insights from three case studies in Brazil and France. *Landscape Ecology*, 1–18.

- Thompson, S. C. G., & Barton, M. A. (1994). Ecocentric and anthropocentric attitudes toward the environment. *Journal of Environmental Psychology*, 14, 149–157.
- Vieira, S., de Camargo, P. B., Selhorst, D., Da Silva, R., Hutyra, L., Chambers, J. Q., ... Wofsy, S. C. (2004). Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia*, 140, 468–479.
- Wang, H., & Fu, R. (2007). The influence of Amazon rainfall on the Atlantic ITCZ through convectively coupled Kelvin waves. *Journal of Climate*, 20, 1188–1201.
- Whitmore, T. C. (1989). Canopy gaps and the two major groups of forest trees. *Ecology*, 70, 536–538.
- Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., ... Díaz, S. (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, 91, 3664–3674.
- Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., ... Prohaska, N. (2016). Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. *Science*, 351, 972–976.
- Wu, J., Kobayashi, H., Stark, S. C., Meng, R., Guan, K., Tran, N. N., Miura, T. (2018). Biological processes dominate seasonality of remotely sensed canopy greenness in an Amazon evergreen forest. *New Phytologist*, 217, 1507–1520.

Chapter 4

TREES UNDER CANOPY OF TERRA FIRME FOREST IN CENTRAL AMAZONIA ARE MORE TOLERANT TO LOCAL AND LARGE-SCALE CLIMATE CHANGES

Abstract

Currently, the Brazilian Amazonian forest has been standing out by the increasing deforestation rates and forest habitat loss. Consequences of extremely relevance for the planet's balance maintaining and human well-being, considering its key role in conservation biodiversity and water cycling through its ecosystem services. Thus, assessing how trees occupying different forest vertical profiles are being affected by local and large-scale climate changes will be fundamental to understanding the Amazon forest resilience due to the contemporary environmental problematic. In this paper, we use tree rings of *Theobroma sylvetsre* Mart. (Malvaceae), occupying the lower and intermediate vertical profile of *terra firme* type of forest in Central Amazonia as bioindicators of local and large-scale climate changes. Through dendrochronological analysis we found that *Theobroma sylvestre* trees are more tolerant to climate changes caused by edge effects and Atlantic ocean warming, compared to *Scleronema micranthum* (Ducke) Ducke (Malvaceae), a typical canopy tree. Large-scale climate phenomena related to increased rainfall was more correlated whit *T. sylvestre* trees in interior of the forest, suggest that individuals not exposed to edge effects would be more benefit by the intensification of the hydrological cycle during the last 30 years. We highlight the tree rings as relevant bioindicators of the local and large-scale climate influences that tropical trees experience throughout their lives. Knowledge that would benefit Amazon forest management and restoration practices in futures scenarios of forest fragmentation and global warming. However, we would like to expand the study to a larger number of species, looking for clarify and confirm these issues.

Keywords: Tree rings; Amazonian forest fragmentation; Sub-canopy; Climate changes; Pacific decadal oscillation; Atlantic Ocean warming; Biological Dynamics of Forest Fragments Project

Introduction

The greatest wealth of the Amazon forest are revealed through its magnificent biodiversity, encompassing approximately 16,000 tree species distributed among 390 billion individuals, although $\pm 50\%$ are represented by only 227 species (Ter Steege et al., 2013a). Associated with your continental extension, comprising the world's largest rainforest and river system (Wesselingh et al., 2010).

This union sustain one of the major centers of deep atmospheric convection and heavy rainfall on the planet (Barichivich et al., 2018), contributing with $\sim 17\%$ of total global freshwater input to the oceans (Callede et al., 2010), being a relevant source of water vapor for the entire climate system (Nobre et al., 2009a), able to release 20 trillion liters of water a day (Nobre, 2014).

According to Marengo and Lovejoy (2018), the most important influence of Amazon moisture is the contribution of dry season Amazon evapotranspiration to rainfall in southeastern South America through circulation of Low-Level Jet (Marengo et al., 2004) and Aerial rivers and lakes (Arraut et al., 2012).

In Brazil, the Amazon forest evapotranspiration are fundamental for the water supply of extra-Amazonian hydroelectric reservoirs and most productive agricultural regions of the country (Fearnside, 2003). Thus, changing the levels of precipitation over these regions of Brazil would result in substantial monetary losses for the country, which has 65% of its electrical matrix consisting of hydroelectric power (MME, 2018) and 25% of its gross domestic product (GDP) dependent on agriculture and agribusiness (CEPEA, 2019).

Currently, the Brazilian Amazon conservation are strongly weakened by promises and actions of the Brazil's new president, that threaten Brazilian Amazonian forest and the traditional people who inhabit it (Ferrante and Fearnside, 2019). Reflecting in the increase of Brazilian Amazon forest deforestation by approximately 88% compared to 2018 (INPE, 2019), and the ongoing potential increases of legal deforestation rates after Brazilian Forest Act revision, that favors the reduction size of the legal reserves for nature protection from 80% to 50% in Amazonian private properties (Freitas et al., 2018).

The current advances in Amazon forest fragmentation has a strong potential to alter the local and large-scale climate. Newly created edge of forest fragments, favored the light incidence, temperatures increases, humidity reduction, vapor pressure deficits increases, depleted soil moisture, favoring drought stress (Camargo and Kapos, 1995; Pinto et al., 2010). These alteration can drastically reduce forest evapotranspiration rates, affecting downwind rainfall and hence, the Amazon basin water cycle (Jose A Marengo, 2006; Zemp et al., 2014; Marengo and Espinoza, 2016). Thus, considering that 25% of the rainfall in the Amazon Basin is recycle from the forest surface itself (Angelini et al., 2011), forest fragmentation can induced serious consequences on maintenance and balance of the world's largest rainforest. Influencing the national and international political relations, fundamental for environmental conservation and human well being.

Besides exerting influence on the climate system, the Amazon forest is also strongly influenced by him. Studies showed that the reduction (increase) of rainfall and extreme droughts (floods) over the Amazon forest are related to the warming (cooling) of the Equatorial Pacific sea surface temperature by the El Niño (La Niña) phenomenon (Schöngart et al., 2004; Marengo and Espinoza, 2016; Panisset et al., 2018). More recent findings have highlighted the role of increasing Atlantic sea surface temperature in hydrological cycle

intensification over the Amazon basin especially during the rainy season (Gloor et al., 2013, 2015; Barichivich et al., 2018; Espinoza et al., 2019). In this sense, to believe that projections of 1.5 °C global warming (Intergovernmental Panel on Climate Change 2019) won't influence these large-scale climate phenomena, may seem very simplistic and dangerous, considering the current environmental conjuncture.

Therefore, recognizing the role of Amazonian trees in climate regulation as water supply and the increased of deforestation rates associated with global warming. The goal in this paper was to reveal through a dendrochronological approach, how *Theobroma sylvestre* Mart. (Malvaceae) trees, typically located at lower position in the vertical profile of *terra firme* type of Amazonian forest are being influenced and respond to local and large-scale climate variability along their life's cycle, in order to address the following questions:

- (i) *Theobroma sylvestre* trees exposed to edge effect are more sensitive to local and large-scale climate variability?
- (ii) Local and large-scale climate variability exert divergence influences on trees occupying different Amazon forest vertical profile exposed and not exposed to edge effects?

Materials and Methods

Study and sampling areas

The present study was carried out in the Biological Dynamics of Forest Fragments Project (BDFFP) study sites, the world's largest and longest-running experimental study of tropical habitat fragmentation (Lovejoy et al., 1986; Laurance et al., 2018). The BDFFP is located 80 km North of Manaus, Brazil (2°30'S, 60°W) and covers an area of ~1000 km². A description of the project and the location of all fragments and control areas can be found in Gascon and Bierregaard (2001). The total annual precipitation ranges from 1900 to 3500 mm with a moderate, but remarkable dry season (<100 mm/month) from June to October (Laurance et al., 2018).

Under a phytophysiognomy-based definition, the sampled area is typified mature forest of *terra firme*, a term used for non-flooded Amazonian forests, which represents 80% of the Biome (Pires and Prance, 1985). In general, four strata define a forest structure (understory, sub-canopy, canopy and emergent) with a 25-35 m canopy on average and with emergent trees that can reach up to 45 m, representing a tree biodiversity of about 1,300 species (>10cm DBH) (BDFFP personal communication, 2019).

For the present study, two BDFFP reserves were visited to collect wood samples from trunks of *Theobroma sylvestre* trees exposed and not exposed to edge effects (Fig 20). Trees exposed to edge effects were located close to the edge or at most, 300 m far from any edge in the Porto Alegre reserve, specifically at the 100-ha reserve (2°22'2.82"S, 59°58'31.63"W). The reserve was isolated and created in August of 1983, by cutting and burning the surrounding pristine forest to establish new pasture lands. We defined the penetration distance of edge effects up to 300 m because increasing tree mortality associated to forest fragmentation can be detectable until this distance (Laurance et al., 2018). Trees not exposed to edge effects were sampled at Esteio reserve, at the continuous forest located within the Km 41 reserve (2°26'15.52"S, 59°46'1.25"W). The reserve was created in 1984, and the forest was kept intact and used as one of the control areas.

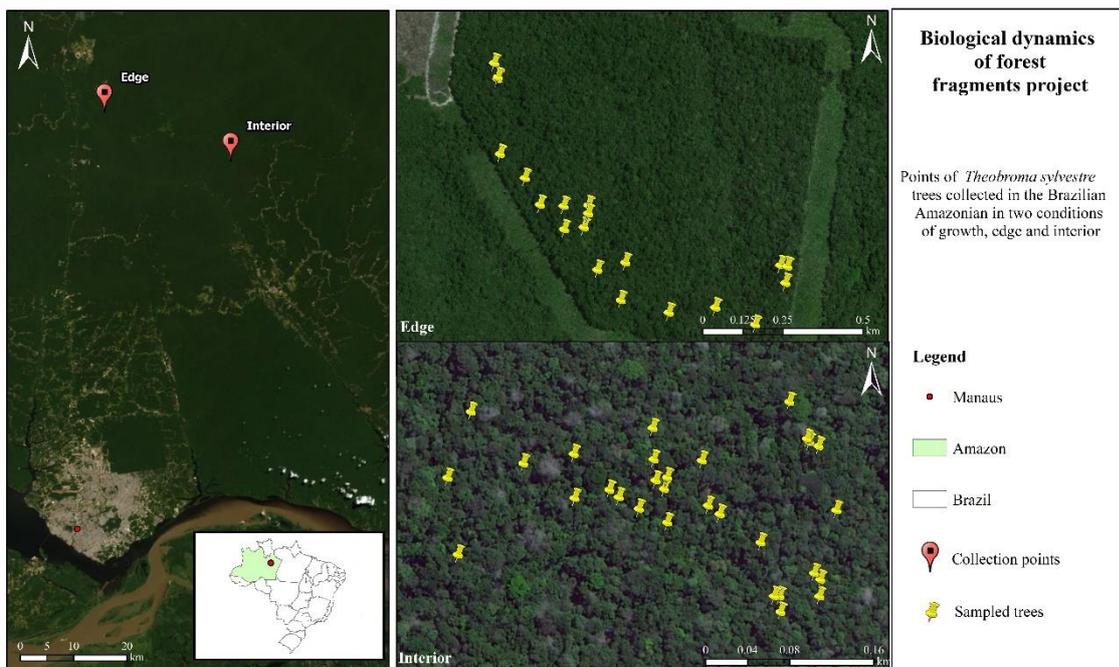


Figure 20. Location (red dots) of the two study sites at the Biological Dynamics of Forest Fragments Project (BDFFP) in *terra firme* forests of Central Amazonia (left). Yellow dots indicate sampled trees in edge areas of the Porto Alegre reserve (upper right map) and in continuous forest at the Esteio reserve (lower right map).

Theobroma sylvestre tree-ring analysis

For dendroecological analyses we take wood samples between April to October 2016 from a total of 50 *Theobroma sylvestre* trees, 20 growing close to the forest edge and 30 in the interior of the continuous forest. The sampled trees were in good phytosanitary condition and did not presented liana infestation (Fig. 2A) Three radial cores were collected for each tree at

DBH using increment borers (diameter = 5.1 mm). Each core was polished with different abrasive sand paper (from 80 to 600 grains/cm²) with the aim of revealing tree ring boundaries. Subsequently, all tree rings were identified and dated with the aid of a stereomicroscope according to the classic method using narrow rings as pointer years (Stokes and Smiles, 1996). After identification, all tree-ring series were scanned at a resolution of 2400 dpi by an HP G4050 scanner. Measurements of tree-ring widths were performed with a precision of 0.001 mm through the software Image J.

To evaluate dating accuracy, the temporal series of ring widths were compared within and among trees at each site. Both visual and statistical cross dating were performed. Visual cross dating was done working with ring-width bar plots, and statistical cross dating was tested using COFECHA software (Holmes, 1983). COFECHA uses segmented temporal series correlation techniques to assess the quality of cross dating and measurement accuracy in the tree ring time series (Grissino-Mayer, 2001).

After evaluating the dating in COFECHA software, we sought to construct master chronologies for each site that would increase the retention of common growth signals. According to Cook and Kairiukstis (1990), spline functions with length between 67 and 75% of the series are able to remove biological growth trends related to high frequency variances. To build site chronologies, time series were detrended and standardized using a smoothed cube spline function with 50% frequency-response cut-off for 65% of the length of each series in dplR package in R Software (Bunn, 2008). The standardization of the series was performed by dividing the width of the tree ring by the growth model of the smooth cubic spline function, producing dimensionless ring-width indices (RW) (Bunn and Korpela, 2017). The quality of the chronology was evaluated by the value of Rbar and EPS (expressed population signal), both calculated with the dplR package on R Software (Bunn, 2008). The Rbar is the average correlation coefficient resulting from comparing all possible segments of a predetermined length among all the series included in the chronology (Briffa, 1995). The EPS values provided information that confirmed the existence of common signals among trees, EPS values higher than 0.80 indicate that the limiting factor of growth in the chronology probably is homogenous (Mendivelso et al., 2014).

Growth-climate analyses

To explore growth-climate patterns among trees located close to the edges and trees located in the forest interior, the ring-width data were converted into basal area increment (BAI). BAI is considered a more informative measure of tree growth trends in terms of total

biomass production (Peñuelas et al., 2011; Phipps and Whiton, 1988), to explore the differences in growth-climate patterns between trees located close to the edges and trees located in the forest interior. Ring-width was converted to BAI according to the following standard formula: $BAI = \pi (R_n^2 - R_{n-1}^2)$, where R is the tree radius and n is the growth ring formation year. To calculate BAI we used the `bai.out` function in `dplR` package in R Software (Bunn, 2008; Bunn & Korpela, 2017).

After transforming growth ring width in BAI, we evaluated, by spatial correlations, the influence of sea surface temperature (SST) from the Atlantic (A.SST) and Pacific (P.SST) Oceans on tree BAI using data available from the Climate Explorer Website (<http://climexp.knmi.nl/>) from the KNMI (Royal Netherlands Meteorological Institute), through HadISST1 1.0° special field correlation. Hence, we divided the time series into two periods, prior (1970 to 1982) and after forest fragmentation and, consequently, edge creation (1983 to 2015) analyzing the influence of the period before the dry season (March to June), the period of the core dry season (July to October), and the period after the dry season with the onset of rainfall (November to February).

Seeking to evaluate how the local and large-scale climate variables as correlate with basal area increment of trees exposed and not exposed to the edge effects, before, during and after the dry season, before and after forest fragmentation and Atlantic Ocean warming. Historical series (1970 to 2015) of precipitation (CRU TS 4.02, 0.5° - 2.27°-2.47°S and 59°-60°W), North Atlantic sea surface temperature (NA.SST, 6 - 22°N and 80 - 15°W), South Atlantic sea surface temperature (SA.SST, 25°S - 2°N and 35°W - 10°E) and Pacific sea surface temperature (P.SST, 50°S - 20°N and 180°W - 82°W) obtained from the Climate Explorer Website (<http://climexp.knmi.nl/>) and The Pacific Decadal Oscillation (PDO) obtained from the National oceanic and atmospheric administration (NOA) (<https://www.ncdc.noaa.gov/teleconnections/pdo/>), were used in the construction of a correlation analysis (Pearson; $P < 0.05$) in R Software (R core Team, 2017).

Results

Tree-ring chronologies of *Theobroma sylvestre*

The tree rings of *Theobroma sylvestre* in edge and interior site were distinct and characterized by growth layers demarcated by fiber flattening of their wall radial sections and local tangential widening of the ray cells (Fig 21). The master chronology (Fig 22) was built from tree-ring widths covering a period of 69 years (1947-2015) for trees located close to the edge and 57 years (1959-2015) for trees located at the interior of the forest, confirming the

presence of the trees before forest fragmentation and edge creation in 1983. The cross-dating quality and accuracy in the measurements of the tree rings was confirmed by the correlations, $EPS > 0.80$ and $Rbar > 0.3$ values, indicating a common growth pattern in edge and interior site. The descriptive statistics of the chronologies are presented in Table 9

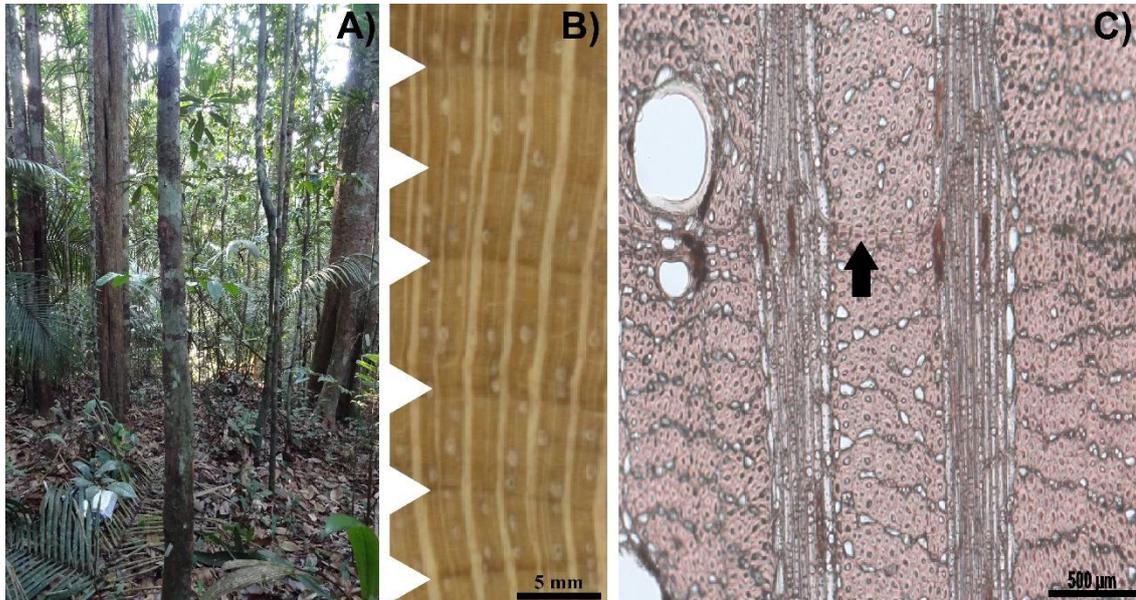


Figure 21. A) *Theobroma sylvestre* tree in the edge at Biological Dynamics of Forest Fragments Project site; B) Macro and C) microscopic images of the transverse wood section evidencing the tree ring anatomy characterized by growth layers demarcated by fiber flattening and the local tangential expansion of rays. White triangles indicate the growth-rings limits and black arrow indicate the fiber flattening.

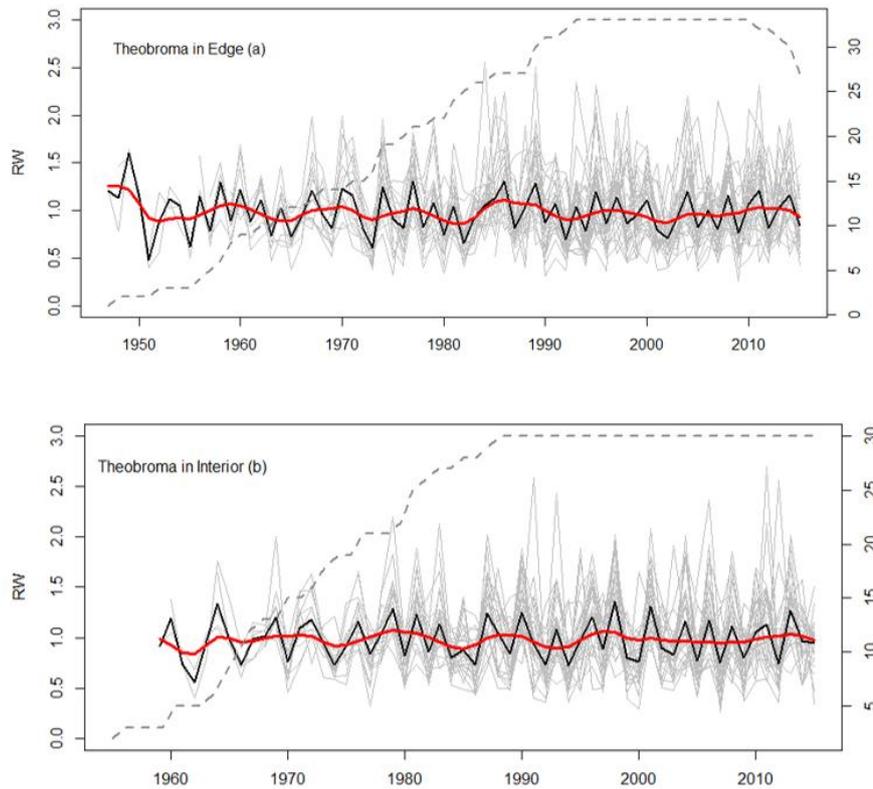


Figure 22. Residual tree-ring chronology of *Theobroma sylvestree* trees for Edge (a) and Interior (b) locations in *terra firme* type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. Grey solid line: individual average time series; black line: residual tree-ring master chronology; grey dotted line: number of radial cores used for the index calculation; red line: standardization of master chronology by a 10% smoothed spline curve.

Table 9. Descriptive statistics of the chronologies of *Theobroma sylvestree* trees located close to the edge and in the interior of the forest at the Biological Dynamics of Forest Fragmentation Project in Central Amazonia.

Variables	Edge	Interior
No. trees/No. radial cores	17/33	19/30
Mean ring width \pm SD (cm)	0.08/0.02	0.08/0.04
Time span	1947- 2015	1959-2015
Age \pm SD	50/11	43/8
Mean sensitivity	0.36	0.39
Series intercorrelation	0.50	0.51
Rbar (\pm SD)	0.32/0.03	0.31/0.02
Period with EPS \geq 0.80	1955-2015	1965-2015

Growth-climate analyses

After the construction of the chronologies and the growth-ring annuity confirmation, we sought to compare edge and interior population climate-growth patterns with similar age and diameter structure, seeking to avoid ontogenetic influences. For this, 13 trees located close to the edge and 11 trees located in the interior of the forest representing populations of similar ages and diameter classes, corresponding a common growth period (1970–2015) were selected (Table 10). Growth-climate analyses were performed for these subsamples (24 individuals), converting the ring width into basal area increment (BAI) (Fig 23).

Table 10. Age and diameter at breast height (DBH) of *Theobroma sylvestre* trees at edge and interior sites in *terra firme* type of forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia selected for growth pattern analyzes.

Year	Edge		Interior	
	DBH	Age	DBH	Age
1970	1.09 (SD ± 0.7)	10 (SD ± 4)	1.02 (SD ± 0.7)	7 (SD ± 5)
1982	2.53 (SD ± 1.4)	16 (SD ± 9)	2.52 (SD ± 1.5)	15 (SD ± 7)
2015	8.03 (SD ± 1.4)	49 (SD ± 9)	7.05 (SD ± 2.7)	48 (SD ± 7)

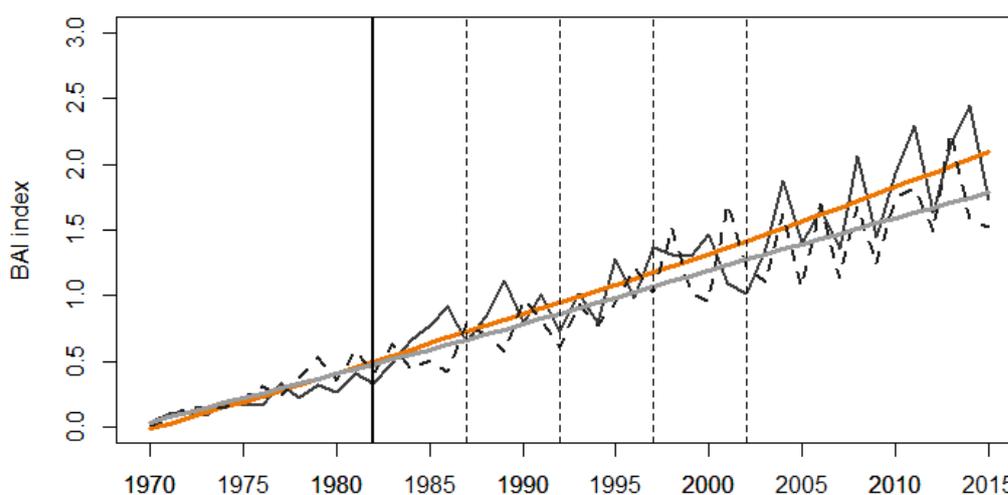


Figure 23. Dominant basal area increment (BAI) index patterns of *Theobroma sylvestre* trees located close to the edge (solid black lines) and in the interior of the forest (dashed black line) in *terra firme* forest at the Biological Dynamics of Forest Fragments Project in Central Amazonia. Orange line: standardization by a 30% smoothed spline curve of BAI chronology of trees located close to the edge; gray line: standardization by a 30% smoothed spline curve of BAI chronology of trees in the interior of the forest; vertical solid black line: edge creation year (1982); vertical dashed black line: five, ten, fifteen and twenty years after edge creation.

Spatial correlation analyzes (Fig 24 and 25) revealed that prior to the increase of the Atlantic sea surface temperature (A.SST) and the forest fragmentation, the basal area increment of *Theobroma sylvestre* trees was more influenced by the South Atlantic sea surface temperature (SA.SST) and by the Pacific sea surface temperature (P.SST). The correlations with SA.SST were mainly negative and more intense before (Mar-Jun) and after

(Nov-Feb) the dry period. And the correlations with P.SST were predominantly positive previously (Mar-Jun), during (Jul-Oct) and after the dry period (Nov-Feb).

After the edge creation and increase of A.SST since 1983, it is remarkable the greater influence of NA.SST on the growth dynamics of the specie. Presenting strong positive correlations before, during and after the dry period. However, it is possible to verify that the spatial correlations between NA.SST and the trees not exposed to edge effects presented higher magnitudes compared to the trees near the edge.

The observed results through the correlation analysis (Fig 26) corroborated with those found by the spatial correlations. Confirming the strong relationship with the Pacific Ocean prior to 1983 and with the Atlantic ocean after the edge creation and increases of A.SST since 1983.

Previously the forest fragmentation and increases of A.SST (1970 to 1982), trees that would be exposed to edge effects, showed statistically significant and positive correlations only with the Pacific sea surface temperature (P.SST), predominantly during the dry season (July to October). Exhibiting, values of +0.66 with PDO.jul.oct, +0.66 with P.SST.jul.oct and +0.059 with PDO.mar.jun.

The predominance of positive correlations with P.SST during the dry season before to 1983 was also confirmed for trees never exposed to edge effects (TI.bai -PDO.jul.oct +0.63 and P.SST.jul.oct +0.67). Although negative correlations with AS.SST prior to the dry season (AS.SST.mar.jun -0.059) are also revealed.

It is interesting to observed that after edge creation and increases in A.SST since 1983, correlations with P.SST become negative and correlations with A.SST became positive. However, positive correlations with NA.SST after 1983, were identified only in trees not exposed to edge effects. Being observed in all analysed periods (NA.SST.mar.jun +0.49, NA.SST.jul.oct +0.46 and NA.SST.nov.feb +0.40). Corroborating with the higher intensity of NA.SST in trees far from the edge, demonstrated by spatial correlations after 1983.

The Pacific sea surface temperature influence on tree growth dynamics after 1983, was exerted only by the lower frequency and interdecadal scale phenomenon (PDO). Presenting negative correlations with trees exposed to edge effects, previously (PDO.mar.jun -0.54), during (PDO.jul.oct -0.61) and after (PDO.nov.feb -0.59) the dry period. And with trees located in interior of continuous forest, previously (PDO.mar.jun -0.39) and during (PDO.jul.oct -0.51) the dry period.

Statistically significant correlations between rainfall and trees basal area increment, were only confirmed before edge creation and A.SST increases. Presenting statistically

significant and negative values (-0.59) just between March to June rainfall and trees never exposed to edge effects (TI.bai and CRU.mar.jun).

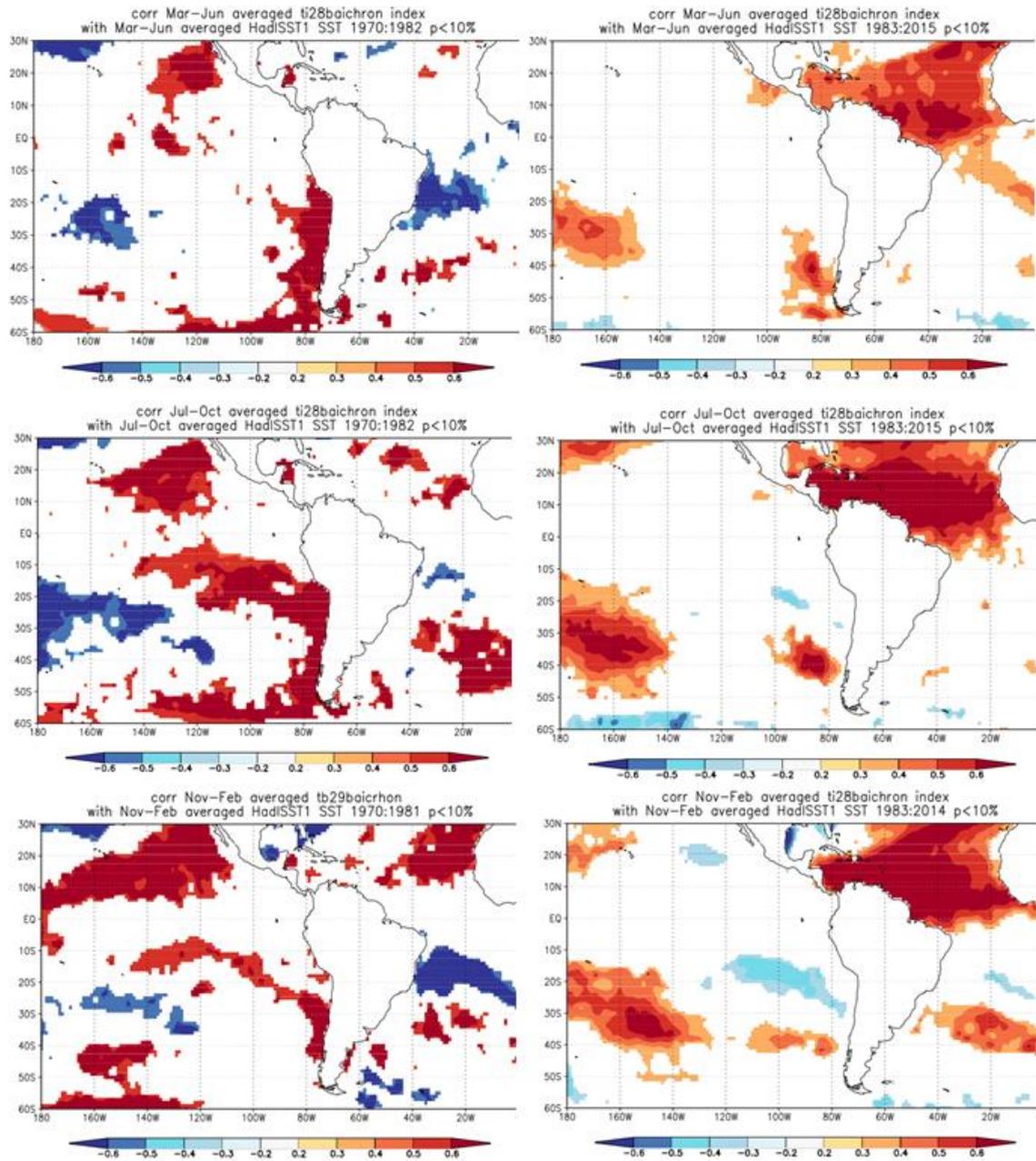


Figure 24. Spatial correlations between the Atlantic sea surface temperature (A.SST) and the basal area increment (BAI) of *Theobroma sylvestree* trees not exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia, before (left side) and after (right side) forest fragmentation, considering the period before (Mar – Jun), during (Jul – Oct) and after (Nov – Feb) the dry season.

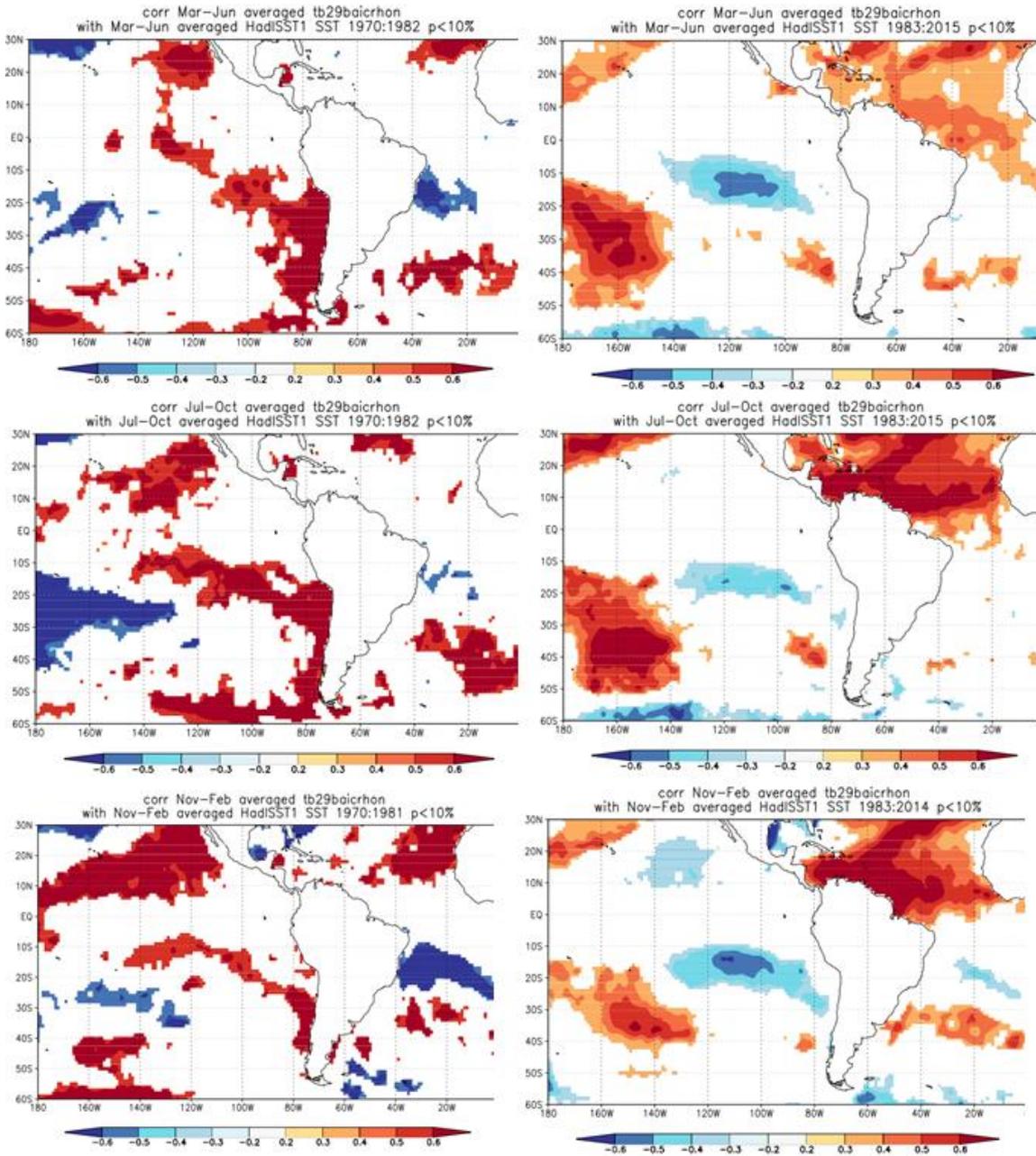


Figure 25. Spatial correlations between the Atlantic sea surface temperature (A. SST) and the basal area increment (BAI) of *Theobroma sylvestri* trees exposed to edge effects at the Biological Dynamics of Forest Fragments Project in Central Amazonia, before (left side) and after (right side) forest fragmentation considering the period before (Mar – Jun), during (Jul – Oct) and after (Nov – Feb.) the dry season.

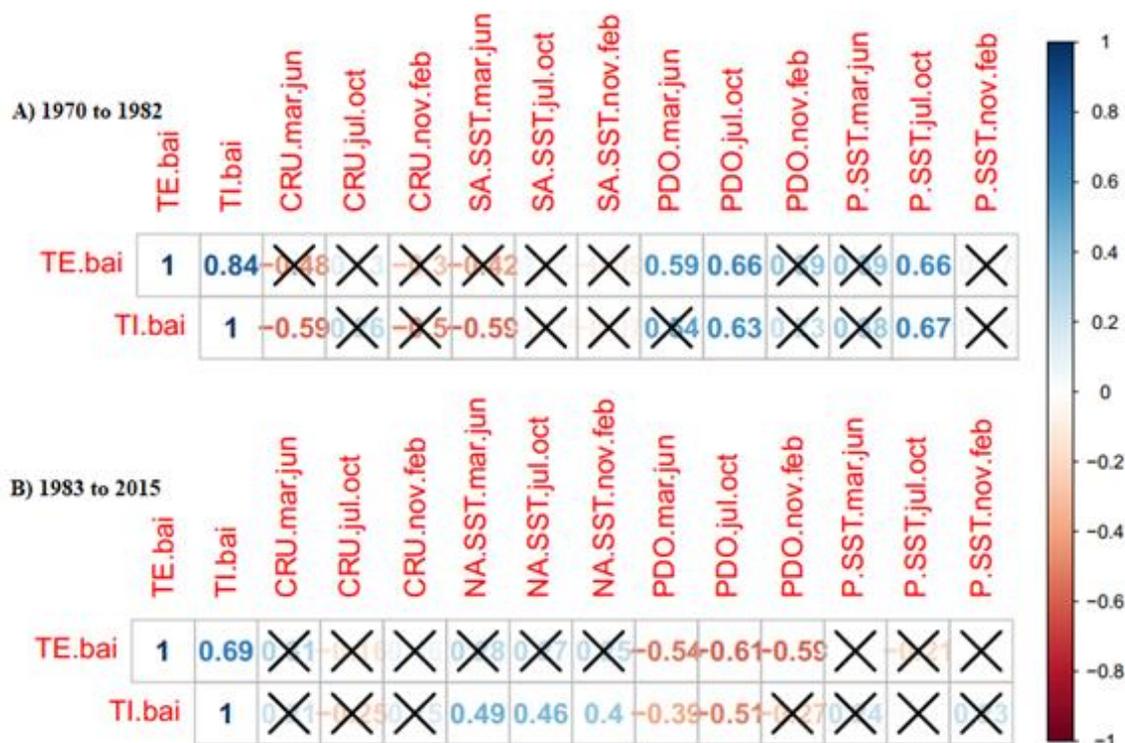


Figure 26. Correlation analysis constructed through Pearson correlation coefficient ($P < 0.05$), previously forest fragmentation (A) and after forest fragmentation (B), between historical series of basal area increment rates of trees exposed to edge effects (TE.bai), basal area increment rates of trees not exposed to edge effects (TI.bai), precipitation (CRU), South Atlantic sea surface temperature (AS); North Atlantic sea surface temperature (NA); Pacific decadal oscillation (PDO) and Pacific sea surface temperature (P.SST), before de dry season (mar.jun), during the dry season (jul.oct) and after de dry season (nov.feb). X indicated de absence of significance statistic ($P > 0.05$).

Discussion

The observed results through correlation analysis were able to reveal a strong large-scale climate phenomenon influence on *Theobroma sylvestri* trees growth during the 45 years evaluated (1970-2015).

Among these large-scale climate phenomena, we can highlight the increase in the Atlantic sea surface temperature since 1980 (Gloor et al., 2015). Manifested by a combination of factors, including the changes in radiative incidence, influenced by anthropic actions as the greenhouse gases increase (Li et al., 2016) and by natural variation of the Atlantic Multidecadal Oscillation (AMO) currently characterized by a positive (warm) phase (Barichivich et al., 2018; Gray et al., 2004).

This increase in the Atlantic sea surface temperature are favoring the Amazonian rains intensification mainly during the rainy season, by atmospheric water vapor import from the warming tropical Atlantic (Gloor et al., 2013). Beside a slight rainfall reductions during the dry season (Gloor et al., 2013), and increased of dry days frequency between the end of the

dry season and the beginning of the rainy season (September to November) (Espinoza et al., 2019), induced by northward displacement of the intertropical convergence zone (Cox et al., 2008; Yoon and Zeng, 2010; Marengo and Espinoza, 2016).

Although *Theobroma sylvestre* trees, located in the lower and intermediate vertical profile of *terra firme* Amazonian forest are strongly spatial correlated with the NA.SST since 1983, previously, during and after the dry period (Figs. 24 and 25). The forest fragmentation and edge creation, apparently did not potentiated the negative effect of rainfall reduction during the dry season on *T. sylvestre* tree growth after the NA.SST warming. Considering that significant Pearson correlations with NA.SST in dry period after 1983, were only observed in trees located in the forest interior. Furthermore, *T. sylvestre* trees exposed to edge effects, showed an 11% increase in basal area increment rates after NA.SST warming and edge creation (Albiero-Júnior et. al 2019b Submitted to the journal: Forest Ecology and Management). Suggesting that large-scale climate effects related to increased NA.SST (reduced rainfall and increased frequency of dry days in dry period), and the local climate changes induced by edge effects (e.g elevate temperature, reduced humidity and increased vapor pressure deficits) (Camargo and Kapos, 1995; Malcolm, 1998; Pinto et al., 2010), seem to have little influence on the growth dynamics of trees located in lower canopy positions.

The positive and significant correlations before 1983, with the Pacific Ocean during the dry period (PDO.jul.oct and P.SST.jul.oct) in trees exposed and not exposed to edge effects, reinforce the low influence of rainfall reduction during the dry period on the *T. sylvestre* trees growth dynamics occupying the lower and intermediate vertical profile of *terra firme* forest in Central Amazonia. Period when the Pacific equatorial waters were more warmer, featuring the positive phase of the PDO, favoring the increase of El Niño events (Andreoli and Kayano, 2005) and consequently increasing drought events.

On the other hand, increased tree growth in lower and intermediate forest vertical profile during the dry season, may also be driven by increased light gaps caused by canopy seasonal variations, considering that the Amazon canopy layer abscission mainly occurs in late dry season, favoring the light input in the understory (Tang and Dubayah, 2017).

Opposite results were observed for *Scleronema micranthum* (Ducke) Ducke, a typical canopy trees, that presented after the edge creation and increases of the NA.SST, greater sensitivity to rainfall reduction, decreasing the basal increment rates during the dry season (Albiero-Júnior et al., 2019a).

Therefore, we propose that trees occupying the lower canopy positions in Amazonian *terra firme* forest, can be less sensitive to rainfall reduced in dry season, compared to trees

located in the forest canopy. What can be justified by the greater vulnerability to drought observed in taller and large trees occupying the forest canopy, that need to deal with higher vapor pressure deficit (VPD), higher hydraulic path length resulting in lower xylem resistance to embolism (Brum et al., 2019; McDowell and Allen, 2015).

Trees that dominate the forest understory, have shallow roots with access to shallow soils with lower water potentials, and compensate this limitation presenting greater xylem resistance to embolism (Brum et al., 2019) and anisohydric stomatal control strategy, implying a weaker stomatal control, markedly reducing their water potential following the evaporative demand during the day (Tardieu and Simonneau, 1998). Consequently, by dramatically reducing water potential in the hottest hours of the day, anisohydric plants can be considered more drought tolerant (McDowell et al., 2008).

Despite some Amazon trees develop strategies to deal with water reduction, many studies confirm and emphasize the increased strength and extent of drought events on the Amazonian forest (Marengo et al., 2008; Phillips et al., 2009, Duffy et al., 2015; Aragão et al., 2018). As observed in the Central Amazonian basin during 1982, 1987, 2005, 2010 and 2015 years (Sombroek, 2001; Barichivich et al., 2018), related to the increase of NA.SST (1982, 1987, 2005, 2010 and 2015) and de El Niño events (1982, 1997, 2010 and 2015) (Sombroek, 2001, Panisset et al., 2018). Inducing great alteration on the forest functional composition in consequences of large wet-affiliated trees mortality, and recruitment increase of dry-affiliated trees (Esquivel-Muelbert et al., 2019). Potentiating the forest flammability, favoring the releasing of a large amount of carbon to the atmosphere (Nepstad et al., 2004). That is, causing many damages to the forest and human well-being.

However, the intensification of the hydrological cycle and recurrences of severe flooding may be an even more prominent feature in the Amazonian forest hydrology (Gloor et al., 2013; Barichivich et al., 2018; Chaudhari et al., 2019). As observed in the Central Amazonian basin during 1989, 1999 and 2009 years (Marengo et al., 2012), related to La Niña events (1989 and 199) (Espinoza et al., 2013) and the tropical south Atlantic warming (2009) (Chen et al., 2010).

Therefore, recognizing that the increased precipitation over the Amazonian forest are related to the strengthening of Walker cell circulation in response to the Atlantic ocean warming (Barichivich et al., 2018). And the Pacific ocean cooling, modulated by high frequency phenomena at annual intervals (La Niña) and low frequency phenomena at decadal intervals (Pacific Decadal Oscillation – PDO) (Mantua et al., 1997; Molion, 2005; Gloor et al., 2015; Espinoza et al., 2019).

The positive and significant correlations between the basal area increment of trees located in the forest interior (TI.bai) and NA.SST in rainy season (March to June and November to February), can reveal that *T. sylvestre* trees growth in the forest interior, may be favored by increased rainfall as a result of atmospheric water vapor import from the warming tropical Atlantic. Although the absence of statistical significance correlations with rainfall after 1983 cannot confirm this contribution.

Despite we don't initially expected positive and significant correlations between NA.SST in dry season (July to October) and trees located in the forest interior (TI.bai) after 1983, due to rainfall reduction in consequence of Atlantic ocean warming and northward displacement of the intertropical convergence zone (Gloor et al., 2013). These result also can be justify by the canopy seasonal variation, enhancing the light input in the understory by the canopy layer abscission in dry season (Restrepo-Coupe et al., 2013), favoring tree growth in lower forest vertical profile.

According to Tang and Dubayah (2017), understory growth is strongly driven by seasonal canopy variations, as observed in *T. sylvestre* trees during the dry season. In this sense, we believe that canopy phenology is also influencing *T. sylvestre* tree growth during the rainy season. In view of the negative and significant spatial correlations with the South Atlantic sea surface temperature during the rainy season (March to June and November to February) before 1982 in both populations. These results may indicate that leaf growth of the canopy layer, favored by increase rainfall in response to AS.SST warming (Espinoza et al., 2014; Marengo et al., 2012), may be reducing the light incidence in forest understory, affecting the growth of trees in lower canopy position. Negative and significant correlations between trees located in the forest interior and SA.SST from March to June reinforce this justification.

Although the seasonal canopy variations exert a strong influence on *T. sylvestre* growth dynamic, significant and negative correlations after 1983 between PDO and trees exposed to the edge effects during all seasons of the year and with trees not exposed to edge effects before and during the dry season, reinforce the influence that large-scale climate phenomena related to increase of rainfall, are exercising on the growth dynamics of these individuals located in lower and intermediate forest vertical profiles. Considering that since 1999, the cooling of the Pacific sea surface temperature, revealed an emergence of a PDO negative phase, inducing the rainfall intensification in the Amazonian forest (Molion, 2005; Gloor et al., 2013; Espinoza et al., 2019).

It is interesting to note that after 1983, trees located in the interior of the forest showed statistically significant correlations with Pacific and Atlantic Ocean. While trees exposed to edge effects showed statistically significant correlations only with the Pacific (PDO). These results lead us to question whether trees located in forest interior would be benefiting more from the intensification of rainfall compared to trees exposed to edge effects.

Thus, considering that the air near forest edges is drier and hotter and soil moisture was lower (Kapos, 1989; Camargo and Kapos, 1995). One initial explanation for this question would be the edge effects influences, making water resources less available to trees. However, this discussion should be strengthened, considering the complexity of large-scale climate relations on rainfall and droughts in the Amazon forest associated with edge effects. Thus, we highlight the need to extend the study to a larger number of species in order to confirm the major influence of rainfall increase on trees located in the interior of the *terra firme* Amazon forest.

Conclusion

The present study provides new perspectives of the large-scale climate (Atlantic ocean warming and PDO negative phase) and local climate (edge effect) influences on tree growth dynamics locate at different vertical profile of *terra firme* forest in central Brazilian Amazon. Revealing that *Theobroma sylvestre* trees located in the lower and intermediate forest vertical profile, are more tolerant to edge effects and Atlantic ocean warming consequences after 1980, compared to *Scleronema micranthum*, a typical canopy tree. Results that may be associated with the development of drought tolerance strategies in trees that occupy the lower vertical profile of the Amazon forest. Although tree growth in lower forest vertical profiles were more correlated with large-scale climate phenomena related to increased rainfall, canopy phenology can also be an important driver of these individuals' growth. The higher correlation of *T. sylvestre* trees located in the forest interior to large-scale climate phenomena related to increased rainfall (PDO and NA.SST) compared to *T. sylvestre* trees exposed to edge effects, may suggest that individuals not exposed to edge effects would be more benefit by the intensification of the hydrological cycle. Thus, we highlight the need to expand the study to a larger number of species, looking for clarify and confirm these issues. However, our study reinforces the tree rings as relevant bioindicators of the local and large-scale climate influences that trees experience throughout their lives. Providing valuable insight into how climate change and forest fragmentation of the Anthropocene are affecting tree growth

dynamics in different vertical profiles of *terra firme* Amazon forest. Knowledge that would benefit Amazon forest management and restoration practices.

References

- Albiero-Júnior, A., Camargo, J.L.C., Roig, F.A., Schöngart, J., Pinto, R.M., Venegas-González, A., Tomazello-Filho, M., 2019. Amazonian trees show increased edge effects due to Atlantic Ocean warming and northward displacement of the Intertropical Convergence Zone since 1980. *Sci. Total Environ.* 693, 133515.
- Albiero-Júnior, A., Venegas-González, A., Camargo, J.L.C., Roig, F.A., Tomazello-Filho, M., 2019b. Not everything is so bad: tree growth under canopy of terra firme forest in Central Amazonia is favored after forest fragmentation. Submitted to *Journal of Ecology*.
- Andreoli, R. V., Kayano, M.T., 2005. ENSO-related rainfall anomalies in South America and associated circulation features during warm and cold Pacific decadal oscillation regimes. *Int. J. Climatol. A J. R. Meteorol. Soc.* 25, 2017–2030.
- Angelini, I.M., Garstang, M., Davis, R.E., Hayden, B., Fitzjarrald, D.R., Legates, D.R., Greco, S., Macko, S., Connors, V., 2011. On the coupling between vegetation and the atmosphere. *Theor. Appl. Climatol.* 105, 243–261.
- Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Rosan, T.M., Vedovato, L.B., Wagner, F.H., Silva, C.V.J., Junior, C.H.L.S., Arai, E., Aguiar, A.P., 2018. 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nat. Commun.* 9, 1-11.
- Arraut, J.M., Nobre, C., Barbosa, H.M.J., Obregon, G., Marengo, J., 2012. Aerial rivers and lakes: looking at large-scale moisture transport and its relation to Amazonia and to subtropical rainfall in South America. *J. Clim.* 25, 543–556.
- Barichivich, J., Gloor, E., Peylin, P., Brienen, R.J.W., Schöngart, J., Espinoza, J.C., Pattanayak, K.C., 2018. Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. *Sci. Adv.* 4, 85-87.
- Briffa, K.R., 1995. Interpreting high-resolution proxy climate data—the example of dendroclimatology, in: *Analysis of Climate Variability*. Springer, pp. 77–94.
- Brum, M., Vadeboncoeur, M.A., Ivanov, V., Asbjornsen, H., Saleska, S., Alves, L.F., Penha, D., Dias, J.D., Aragão, L.E.O.C., Barros, F., 2019. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *J. Ecol.* 107, 318–333.
- Bunn, A., Korpela, M., 2017. *An introduction to dplR*.

- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124.
- Callede, J., Cochonneau, G., Vieira Alves, F., Guyot, J.-L., Santos Guimaraes, V., De Oliveira, E., 2010. The river amazon water contribution to the atlantic Ocean. *Rev. des Sci. l'eau*. 23, 247-273.
- Camargo, J.L.C., Kapos, V., 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* 11, 205–221.
- CEPEA, D., 2019. Centro de Estudos Avançados em Economia Aplicada, 2019. Disponível em <<http://www.cepea.esalq.usp.br/br>>. Acesso em: 05 Jun. 2019.
- Chaudhari, S., Pokhrel, Y., Moran, E., Miguez-Macho, G., 2019. Multi-decadal hydrologic change and variability in the Amazon River basin: understanding terrestrial water storage variations and drought characteristics. *Hydrol. Earth Syst. Sci.* 23, 2841–2862.
- Chen, J.L., Wilson, C.R., Tapley, B.D., 2010. The 2009 exceptional Amazon flood and interannual terrestrial water storage change observed by GRACE. *Water Resour. Res.* 46, 1-10.
- Cook, E.R., Kairiukstis, L.A., 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer, Amsterdam.
- Cox, P.M., Harris, P.P., Huntingford, C., Betts, R.A., Collins, M., Jones, C.D., Jupp, T.E., Marengo, J.A., Nobre, C.A., 2008. Increasing risk of Amazonian drought due to decreasing aerosol pollution. *Nature* 453, 212-2015.
- Duffy, P.B., Brando, P., Asner, G.P., Field, C.B., 2015. Projections of future meteorological drought and wet periods in the Amazon. *Proc. Natl. Acad. Sci.* 112, 13172–13177.
- Espinoza, J.C., Marengo, J.A., Ronchail, J., Carpio, J.M., Flores, L.N., Guyot, J.L., 2014. The extreme 2014 flood in south-western Amazon basin: the role of tropical-subtropical South Atlantic SST gradient. *Environ. Res. Lett.* 9, 124007-124117.
- Espinoza, J.C., Ronchail, J., Frappart, F., Lavado, W., Santini, W., Guyot, J.L., 2013. The major floods in the Amazonas River and tributaries (Western Amazon basin) during the 1970–2012 period: A focus on the 2012 flood. *J. Hydrometeorol.* 14, 1000–1008.
- Espinoza, J.C., Ronchail, J., Marengo, J.A., Segura, H., 2019. Contrasting North–South changes in Amazon wet-day and dry-day frequency and related atmospheric features (1981–2017). *Clim. Dyn.* 53, 1–18.

- Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienens, R.J.W., Feldpausch, T.R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., 2019. Compositional response of Amazon forests to climate change. *Glob. Chang. Biol.* 25, 39–56.
- Fearnside, P.M., 2003. A floresta amazônica nas mudanças globais. INPA Manaus.
- Ferrante, L., Fearnside, P.M., 2019. Brazil's new president and 'ruralists' threaten Amazonia's environment, traditional peoples and the global climate. *Environ. Conserv.* 9, 1–3.
- Freitas, F.L.M., Sparovek, G., Berndes, G., Persson, U.M., Englund, O., Barretto, A., Mörtberg, U., 2018. Potential increase of legal deforestation in Brazilian Amazon after Forest Act revision. *Nat. Sustain.* 1, 665-670.
- Gascon, C., Bierregaard Jr, R.O., 2001. The biological dynamics of forest fragments project. Lessons from Amaz. *Ecol. Conserv. a Fragm. For.* 2001, 31–42.
- Gloor, M., Barichivich, J., Ziv, G., Brienens, R., Schöngart, J., Peylin, P., Cintra, L., Barcante, B., Feldpausch, T., Phillips, O., 2015. Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. *Global Biogeochem. Cycles* 29, 1384–1399.
- Gloor, M., Brienens, R.J.W., Galbraith, D., Feldpausch, T.R., Schongart, J., Guyot, J.L., Espinoza, J.C., Lloyd, J., Phillips, O.L., 2013. Intensification of the Amazon hydrological cycle over the last two decades. *Geophys. Res. Lett.* 40, 1729–1733.
- Gray, S.T., Graumlich, L.J., Betancourt, J.L., Pederson, G.T., 2004. A tree-ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 AD. *Geophys. Res. Lett.* 31, 12205-12229.
- Grissino-Mayer, H.D., 2001. Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. *Tree-Ring Res.* 57, 205–221.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43, 69–78.
- INPE, 2019. Satellite-based monitoring of deforestation of the Amazon forest/PRODES “Monitoramento da floresta amazônica brasileira por satélite”.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185.

- Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., Meyer, C.F.J., Bobrowiec, P.E.D., Laurance, S.G.W., 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biol. Rev.* 93, 223–247.
- Li, X., Xie, S.-P., Gille, S.T., Yoo, C., 2016. Atlantic-induced pan-tropical climate change over the past three decades. *Nat. Clim. Chang.* 6, 275.
- Lovejoy, T.E., Bierregaard Jr, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown Jr, K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., 1986. Edge and other effects of isolation on Amazon forest fragments. In M. E.Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, Massachusetts. p.257-285.
- Lovejoy, T.E., Nobre, C., 2018. Amazon Tipping Point. *Science Advances* 4, 2340.
- Malcolm, J.R., 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Clim. Change* 39, 487–502.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78, 1069–1080.
- Marengo, J.A., 2006. On the hydrological cycle of the Amazon Basin: A historical review and current state-of-the-art. *Rev. Bras. Meteorol.* 21, 1–19.
- Marengo, J.A., Espinoza, J.C., 2016. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. *Int. J. Climatol.* 36, 1033–1050.
- Marengo, J.A., Nobre, C.A., Tomasella, J., Cardoso, M.F., Oyama, M.D., 2008. Hydro-climatic and ecological behaviour of the drought of Amazonia in 2005. *Philos. Trans. R. Soc. London B Biol. Sci.* 363, 1773–1778.
- Marengo, J.A., Soares, W.R., Saulo, C., Nicolini, M., 2004. Climatology of the low-level jet east of the Andes as derived from the NCEP–NCAR reanalyses: Characteristics and temporal variability. *J. Clim.* 17, 2261–2280.
- Marengo, J.A., Tomasella, J., Soares, W.R., Alves, L.M., Nobre, C.A., 2012. Extreme climatic events in the Amazon basin. *Theor. Appl. Climatol.* 107, 73–85.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.

- McDowell, N.G., Allen, C.D., 2015. Darcy's law predicts widespread forest mortality under climate warming. *Nat. Clim. Chang.* 5, 669.
- Mendivelso, H.A., Camarero, J.J., Gutiérrez, E., Zuidema, P.A., 2014. Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity. *Agric. For. Meteorol.* 188, 13–23.
- MME, 2018. Balanço energético nacional 2018: ano base 2017. Ministério Minas e Energ. (MME), Rio Janeiro, Bras.
- Molion, L.C.B., 2005. Aquecimento global, El Niños, manchas solares, vulcões e Oscilação Decadal do Pacífico. *Climanalise*, CPTEC/INPE.
- Nepstad, D., Lefebvre, P., Lopes da Silva, U., Tomasella, J., Schlesinger, P., Solórzano, L., Moutinho, P., Ray, D., Guerreira Benito, J., 2004. Amazon drought and its implications for forest flammability and tree growth: A basin-wide analysis. *Glob. Chang. Biol.* 10, 704–717.
- Nobre, A.D., 2014. O futuro climático da Amazônia-relatório de avaliação científica. *Articul. Reg. Amaz.* São José dos Campos CPTEC/INPE.
- Nobre, C.A., Marengo, J.A., Artaxo, P., 2009. Understanding the climate of Amazonia: Progress from LBA. *Washingt. DC Am. Geophys. Union Geophys. Monogr. Ser.* 186, 145–147.
- Panisset, J.S., Libonati, R., Gouveia, C.M.P., Machado-Silva, F., França, D.A., França, J.R.A., Peres, L.F., 2018. Contrasting patterns of the extreme drought episodes of 2005, 2010 and 2015 in the Amazon Basin. *Int. J. Climatol.* 38, 1096–1104.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* 20, 597–608.
- Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., 2009. Drought sensitivity of the Amazon rainforest. *Science* 323, 1344–1347.
- Phipps, R.L., Whiton, J.C., 1988. Decline in long-term growth trends of white oak. *Can. J. For. Res.* 18, 24–32.
- Pinto, S.R.R., Mendes, G., Santos, A.M.M., Dantas, M., Tabarelli, M., Melo, F.P.L., 2010. Landscape attributes drive complex spatial microclimate configuration of Brazilian Atlantic forest fragments. *Trop. Conserv. Sci.* 3, 389–402.
- Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon.
- R core Team, R., 2017. R language definition. Vienna, Austria R Found. Stat. Comput.

- Restrepo-Coupe, N., da Rocha, H.R., Hutrya, L.R., da Araujo, A.C., Borma, L.S., Christoffersen, B., Cabral, O.M.R., de Camargo, P.B., Cardoso, F.L., da Costa, A.C.L., 2013. What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network. *Agric. For. Meteorol.* 182, 128–144.
- Schöngart, J., Junk, W.J., Piedade, M.T.F., Ayres, J.M., Hüttermann, A., Worbes, M., 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation effect. *Glob. Chang. Biol.* 10, 683-692.
- Sombroek, W., 2001. Spatial and temporal patterns of Amazon rainfall. *AMBIO A J. Hum. Environ.* 30, 388–397.
- Stokes, M.A., Smiles, T., 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.
- Tang, H., Dubayah, R., 2017. Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure. *Proc. Natl. Acad. Sci.* 114, 2640–2644.
- Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp. Bot.* 49, 419–432.

- Ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C. V., Magnusson, W.E., Molino, J.F., Monteagudo, A., Vargas, P.N., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.H., Vieira, I.C.G., Amaral, I.L., Brienen, R., Castellanos, H., López, D.C., Duivenvoorden, J.F., Mogollón, H.F., Matos, F.D.D.A., Dávila, N., García-Villacorta, R., Diaz, P.R.S., Costa, F., Emilio, T., Levis, C., Schiatti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A.J.D., Piedade, M.T.F., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard C., G.A., Baker, T.R., Cerón, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Paredes, M.R., Chave, J., Lima Filho, D.D.A., Jørgensen, P.M., Fuentes, A., Schöngart, J., Valverde, F.C., Di Fiore, A., Jimenez, E.M., Mora, M.C.P., Phillips, J.F., Rivas, G., Van Andel, T.R., Von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Schutz, A.C., Gonzales, T., Nascimento, M.T., Ramirez-Angulo, H., Sierra, R., Tirado, M., Medina, M.N.U., Van Der Heijden, G., Vela, C.I.A., Torre, E.V., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Giraldo, L.E.U., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Cuenca, W.P., Pauletto, D., Sandoval, E.V., Gamarra, L.V., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G., Silman, M.R., 2013. Hyperdominance in the Amazonian tree flora. *Science* 342, 325-336.
- Wesselingh, F.P., Hoorn, C., Kroonenberg, S.B., Antonelli, A., Lundberg, J.G., Vonhof, H.B., Hooghiemstra, H., 2010. On the origin of Amazonian landscapes and biodiversity: a synthesis. *Amaz. Landsc. Species Evol. A look into past* 419–431.
- Yoon, J.-H., Zeng, N., 2010. An Atlantic influence on Amazon rainfall. *Clim. Dyn.* 34, 249–264.
- Zemp, D.C., Schleussner, C.-F., Barbosa, H.M.J., Van der Ent, R.J., Donges, J.F., Heinke, J., Sampaio, G., Rammig, A., 2014. On the importance of cascading moisture recycling in South America. *Atmos. Chem. Phys.* 14, 13337–13359.

OVERALL CONCLUSIONS

Through dendrochronological analyzes, this thesis present important insights about how trees growths occupying different vertical profile of the *terra firme* forest in central Brazilian Amazonia are being affected and reacting to forest fragmentation and local and large-scale climate changes during their life.

Surprisingly, we found that trees occupying the forest canopy are more sensitive to edge effects and climatic phenomena related to rainfall reduction and water stress. Showing an 18% reduction in growth rates during the first 10 years of fragmentation. An opposite pattern when compared to tree growth dynamics under forest canopy, that presented approximately 6% increases in growth rates during the first 20 years of fragmentation. Results that can be justified by the greater vulnerability to drought observed in taller and large trees occupying the forest canopy, that need to deal with higher vapor pressure deficit, higher hydraulic path length resulting in lower xylem resistance to embolism.

Large-scale climate phenomena related to increase rainfall was more correlated with tree growth in lower forest vertical profile. However, we believe that canopy phenology was also an important driver of these individuals' growth.

We highlight the relevance of tree rings as important bioindicators of the forest fragmentation and local and large-scale climate influences that trees experience throughout their lives. Knowledge that provides new perspectives on Amazon trees resilience after contemporary environmental problematic, marks by forest fragmentation and climate changes, benefiting forest management and restoration practices.