Impacts of experimental drought on community structure and floristic composition of tree saplings in a lowland tropical rainforest in Eastern Amazonia

Impacto da seca artificial na estrutura e na florística da comunidade de plantas em uma floresta tropical na Amazônia oriental

Leandro Valle Ferreira[I], Denise de Andrade Cunha[I], Pia Parolin[II], Antônio Carlos Lôla da Costa[III]

[I]Museu Paraense Emílio Goeldi/MCTIC. Belém, Pará, Brasil

[II]Institut National de la Recherche Agronomique. Paris, França

[III]Universidade Federal do Pará. Belém, Pará, Brasil

Abstract: In order to test the effect of the lower availability of water for vegetation in a tropical Amazonian forest, a long-term research project was created in 2001 called Projeto Seca Floresta (ESECAFLOR). The main objective of the project is to determine how a significant reduction of the available water in the soil, in the long term, can affect the biota. The ESECAFLOR consists of two 1-hectare plots, the experimental plot is covered with 6,000 plastic panels reducing precipitation by 50%. The objective of this work is to compare the floristic and plant structure (< 2 meters high) between the experimental and control of ESECAFLOR plots. There was a significant reduction in species richness and diversity, plant density and height, and a significant change in species composition between experimental plot compared to control. The plant community clearly responded to the reduction of soil moisture in the experimental plot, corroborating the results of some climate models that say rainfall reduction in the Amazon will negatively affect the plant community.

Keywords: Drought effects. Soil water availability. Tree sapling community. Amazon rainforest.

Resumo: Para testar o efeito da menor disponibilidade de água para a vegetação em uma floresta amazônica tropical, foi criado, em 2001, um projeto de pesquisa de longo prazo, denominado Projeto Seca Floresta (ESECAFLOR). Seu principal objetivo é determinar como uma redução significativa da água disponível no solo, em longo prazo, pode afetar a biota. O ESECAFLOR consiste em duas parcelas de um hectare, a parcela experimental é recoberta com 6 mil painéis plásticos, reduzindo a precipitação em 50%. O objetivo deste trabalho é comparar a florística e a estrutura de plantas (< 2 metros de altura) entre a parcela experimental e o controle do ESECAFLOR. Houve redução significativa na riqueza e na diversidade de espécies, na densidade e na altura das plantas, e mudança significativa da composição de espécies entre a parcela experimental em comparação com a de controle. A comunidade de plantas respondeu claramente à redução da umidade do solo na parcela experimental, corroborando os resultados de alguns modelos climáticos segundo os quais a redução de chuvas na Amazônia vai afetar negativamente a comunidade de plantas.

Palavras-chave: Efeito da seca. Disponibilidade de água no solo. Comunidade de plantas. Floresta amazônica.

FERREIRA, L. V., D. A. CUNHA, P. PAROLIN & A. C. L. COSTA, 2017. Impacts of experimental drought on community structure and floristic composition of tree saplings in a lowland tropical rainforest in Eastern Amazonia. **Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais** 11(3): 351-363.
Autor para correspondência: Leandro Valle Ferreira. Museu Paraense Emílio Goeldi/MCTIC. Coordenação de Botânica. Avenida Perimetral, 1901 – Terra Firme. Belém, PA, Brasil. CEP 66077-530 (lvferreira@museu-goeldi.br).
Recebido em 04/03/2015
Aprovado em 22/05/2017
Responsabilidade editorial: Maria de Lourdes Pinheiro Ruivo e Rogério Rosa da Silva

INTRODUCTION

Increasingly severe and frequent droughts may be considered one of the major threats to Amazon lowland rainforests, at the present and even more so in the future (Laurance *et al*., 2001, 2002; Phillips *et al*., 2009). Forests worldwide, and lowland tropical rainforests in particular, will undergo changes in species composition and structure. It remains unclear how quickly tropical vegetation may change (Condit *et al*., 1995).

In recent years several studies have reported possible global changes associated with potential drought (Asner *et al*., 2009; Stickler *et al*., 2009; Stork *et al*., 2009). Global warming might increase the frequency of *El Niño* events (Timmerman *et al*., 1999), an occurrence that would dramatically increase the vulnerability of Amazonian forests to droughts and fires (Laurance & Williamson, 2001; Laurance *et al*., 2002; Cochrane & Barber, 2009). *El Niño*-Southern Oscillation (ENSO) droughts may increase in intensity and frequency, and cause drastic reductions of precipitation (Nepstad *et al*., 2007). Land-atmosphere global climate models predict a widespread dieback of Amazonian forest cover through reduced precipitation (Barlow & Peres, 2008).

Reductions of water in the forest system cause considerable alterations, such as elevated tree mortality, increased litterfall, shifts in plant phenology, and other ecological changes, especially near forest edges, as well as increased forest loss, fragmentation, and regional climate change (Laurance & Williamson, 2001; Nepstad *et al*., 2007). A considerable increase of the susceptibility to forest fires may result from the combined effects of *El Niño*-induced droughts and land-use change, with all consequences on rates of tree mortality, changes in forest structure, biomass loss and carbon emissions (Barlow & Peres, 2004; Righi *et al*., 2009).

The effects of reduced precipitation on vegetation can be drastic (Clark, 2007; Guariguata *et al.*, 2008). Drought strongly decreases growth, biomass, transpiration and photosynthetic activity (Poorter & Markesteijn, 2008; Parolin *et al.*, 2010), and influences phenological rhythms (Borchert *et al.*, 2002). Physiological responses of trees to drought result in changes of vegetation cover, species composition and shifts of dominant functional groups (Condit *et al.*, 1996; Wright *et al*., 2004; Cai *et al*., 2009). Emerging seedlings and saplings may be filtered with a shift towards more drought-tolerant species (Engelbrecht *et al*., 2002, 2007; Bunker & Carson, 2005; Poorter & Markesteijn, 2008) or functional groups. Shifts from trees to lianas may occur, as lianas fix more carbon and use water and nitrogen more efficiently than trees, particularly during seasonal drought, which may confer a competitive advantage to lianas during the dry season (Cai *et al.*, 2009). Thus, changes to drier climates promote increases in both liana abundance and their proportion in the flora (Wright *et al.*, 2004; Nepstad *et al.*, 2007). Also, overall life-history strategies may change, e.g., from opportunistic generalist species vs. shade-tolerant undergrowth specialists, since interactions between life-history, disturbance regime and distribution pattern mediate whether particular species will be exposed to increased extinction risks under climate change (Akcakaya *et al*., 2008).

To test the effects of lower water availability on the vegetation of a lowland tropical rainforest in eastern Amazonian, the ESECAFLOR project was set up with long-term study plots in 2001. ESECAFLOR consists of a simulation of extended extreme drought in an ombrophilous forest. It was established to evaluate the impact of drought on water and carbon cycles. In the present paper, we analyze the effects of simulated drought on forest regeneration. The objective of this study was to compare the floristics (species richness, diversity and species composition) and structure (absolute abundance) of sapling (plants shorter than 2 m) communities in a water-exclusion and a control plot. The aim of the project was to determine how soil water availability affects the structure, floristics, and composition of tree sapling species.

MATERIAL AND METHODS

The Scientific Station Ferreira Penna, also called Caxiuanã, is located in the municipality of Melgaço (1º 13’ 86” S; 48º 17’ 41.18” W), about 411 km west of Belém, in the basin of the

Caxiuanã River and bay in eastern Amazonia (Figures 1A-1B). It is covered by dense ombrophilous lowland primary and secondary forests of different ages (Almeida *et al*., 1993) and two types of floodplain forests, flooded by nutrient-rich white-water rivers (*várzea*) and by nutrient-poor black-water rivers (*igapós*) (Ferreira *et al.*, 2005). The experimental plots were carefully chosen based on tree species composition and under identical conditions of topography and soil. The distance between the plots was 500 m (Da Costa, 2008).

Two plots of 1 ha each (100 x 100 m) were established, one of which was left as it was (control C) while the other one was artificially covered by plastic sheets (experimental E) in 2001 in order to impose an artificial drought on the vegetation (Da Costa, 2008).

In the experimental plot, trenches with depths between 50 and 150 cm were dug, and 6,000 transparent plastic panels that do not impede the passage of light were installed at an average height of 1.5 to 3.5 m above of the ground (Figure 2). These panels direct the falling rain water into gutters, isolated with waterproof plastic and with an inclination of 2 m between one side of the study plot and the other, so that off-flowing water was directed into the trenches. This brought about a 50% exclusion of rain in plot E as compared to the control plot C. The control plot C is used as reference for the experiments carried through in plot E (experimental hectare).

In each of the C and E plot, 20 sub-plots of 2 x 2 m were randomly established, inside of which all saplings between 10 and 200 cm height were inventoried. Species were determined to the finest possible taxonomic level.

The density and height of individuals and species richness and Shannon-Weaver species diversity between the C and E plots were compared using Student's t-test (Zar, 2010).

The difference in the floristic composition between the C and E plots was compared using Principal Coordinates Analysis (PCoA) and tested by Permutational Multivariate Analysis of Variance (PERMANOVA). The results are presented by PseudoF Index that describes

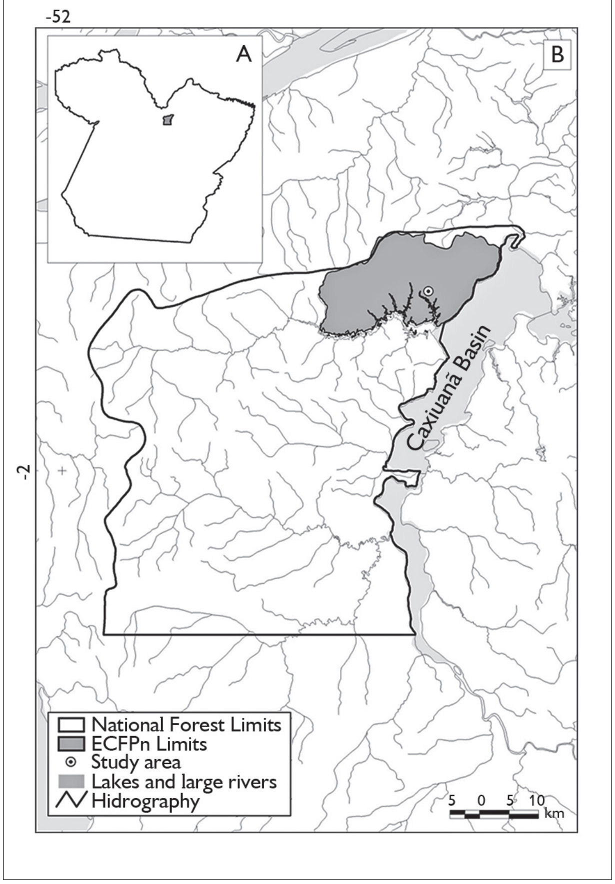

Figure 1. Location of the Ferreira Penna Scientific Station in relation to State of Pará (A) and limits of Ferreira Penna Scientific Station (Estação Científica Ferreira Penna - ECFPn) (B).

Figure 2. Part of 6,000 transparent plastic panels established in the experimental plot. Photo: L. V. Ferreira.

the ratio of between-cluster variance to within cluster variance (Anderson, 2001).

RESULTS

The total number of species was 129 in the C plot and 89 in the E plot. Sixty-two tree sapling species were common to both plots, 67 species occurred exclusively in the C plot, and 23 species occurred exclusively in the E plot (Appendix).

The sapling density was significantly higher in the C plot than in the E plot (Mean (X) = 33; standard deviation (SD) = 12.7) and (X = 17.8; SD = 4.9) (t = 5.00; P = 0.0001), respectively (Figure 3).

The sapling height was significantly greater in the C plot than in the E plot (X = 63.7; SD = 35.9) and (X = 44.8; SD = 12.5) (t = 2.21; P = 0.037), respectively (Figure 3). The species richness was significantly higher in the control plots than in the experimental plots (X = 20.9; SD = 6.7) and (X = 13.2; SD = 2.9) (t = 4.62; P = 0.0001), respectively (Figure 3).

The species diversity was significantly higher in the control plots than in the experimental plots (X = 2.80; SD = 0.37) and (X = 2.26; SD = 0.22) (t = 3.51; P = 0.001), respectively (Figure 3).

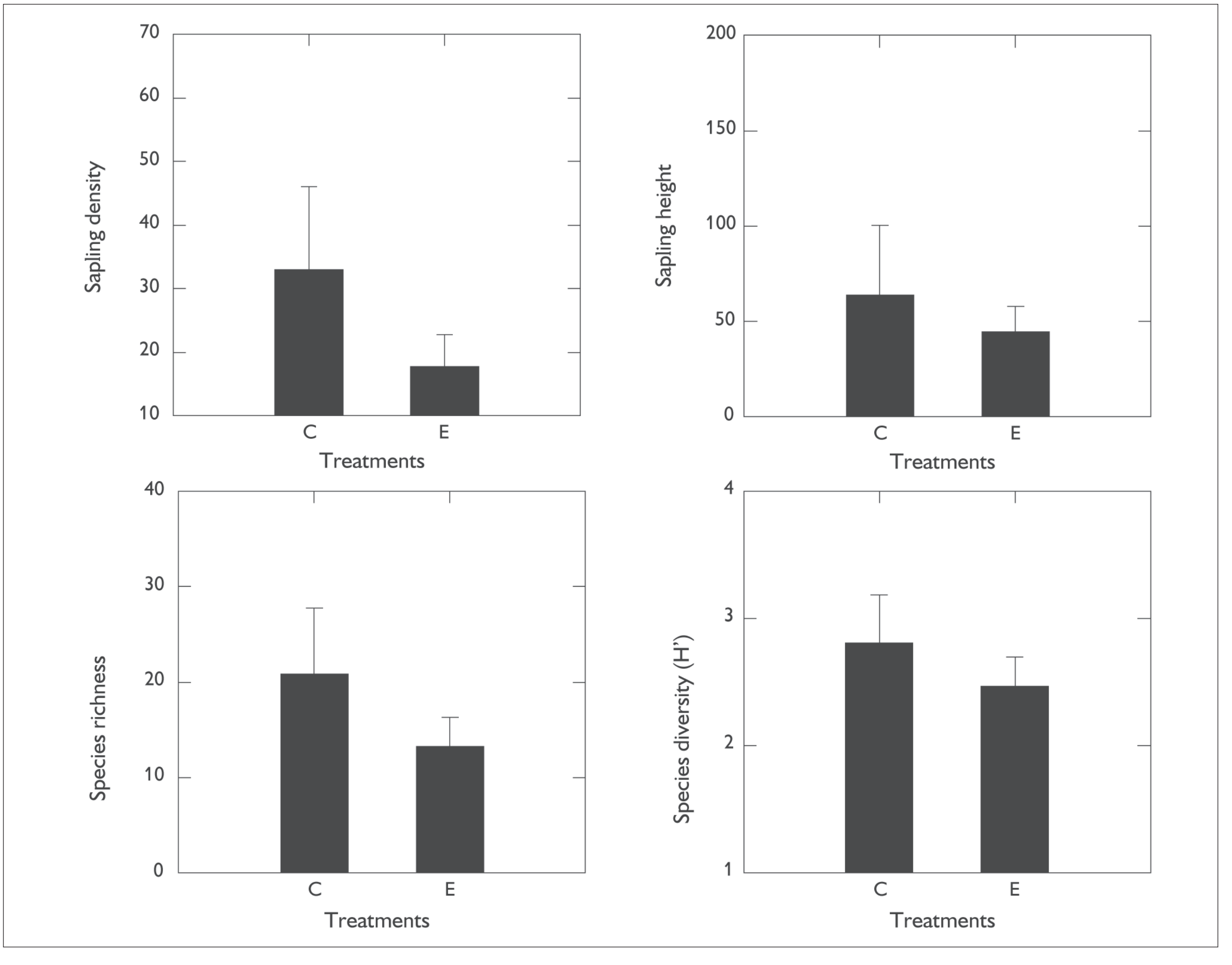

Figure 3. Comparison of sapling density, sapling height, species richness and species diversity between the control (C) and experimental (E) plots.

The species composition was significantly different between the control and experimental plots (PseudoF = 2.17; P = 0.005) (Figure 4).

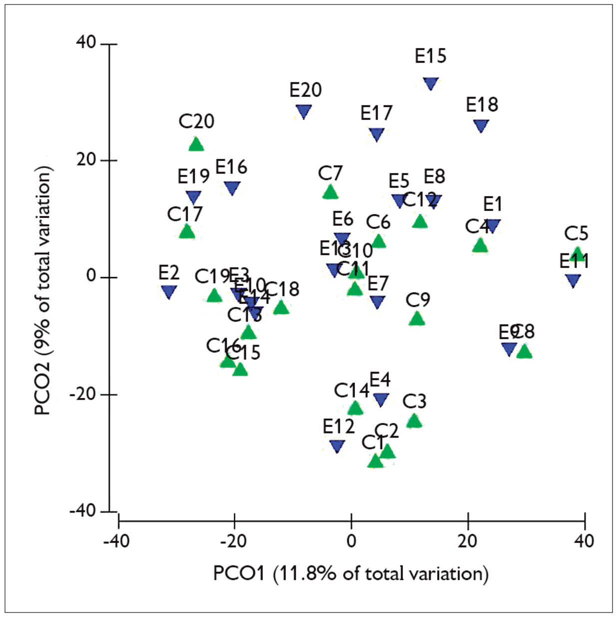

Figure 4. Comparison of species distribution between the control (C) and experimental (E) plots.

DISCUSSION

This study shows that a significant decrease of soil humidity and probably other variables such as temperature and air humidity (Da Costa, 2008), artificially imposed on an Amazonian lowland tropical forest for seven years caused significant changes in species richness and distribution of life forms of the regenerating vegetation.

This is no surprise, as studies from other tropical forests have documented similar changes, but too little is known about the effects of water shortage in Eastern Amazonia, one of the regions which in future will be severely affected by increasing drought (Nepstad *et al.*, 2007). The extreme drought of 2005 – the worst drought in more than a century – was particularly strong in Amazonia (Marengo *et al*., 2008), when the Amazon River floodplains dried up. Although it was an atypical drought caused by warmer ocean temperatures, similar events are recurring more and more frequently and with stronger impacts, mostly linked to ENSO events, causing wildfires which destroy thousands of hectares of forest (Alencar *et al*., 2004).

All changes measured in the drier plots of our study appear to be closely related to the changes of soil humidity. Lower sapling density, height and species richness and species diversity occurred in the plot subjected to water shortage. However, which mechanisms are responsible for these changes in this particular experimental setting cannot be answered with the current state of knowledge. Multiple mechanisms may cause mortality during drought (McDowell *et al*., 2008). A common mechanism for plants with isohydric regulation of water status results from avoidance of drought-induced hydraulic failure via stomatal closure, resulting in carbon starvation and a cascade of downstream effects such as reduced resistance to biotic agents (Saiki *et al*., 2017).

These have to be analyzed in detail for the species in the study plots. The most plausible reasons for the measured changes under drought are sapling mortality and regrowth of species with different ecological requirements and perhaps a broader ecological spectrum. In our study water shortage led to reductions of sapling density at community and population levels, emphasizing the close relationship between water availability, habitat associations, patterns of tree species richness and seedling recruitment and survival (Paine *et al*., 2009). In an experimental approach which did the opposite than our water shortage experiment, supplemental irrigation of a Peruvian rainforest led to enhanced young seedling growth and survival, increasing stem density and diversity (Paine *et al*., 2009), indicating the fundamental role of water in the establishment phase for the local tree species. To date, the responsibility of physiological mechanisms for survival and mortality under drought are still poorly understood and are only postulated to cause the changes measured in our study.

However, not only diversity is positively correlated with water availability at global, continental and regional scales (Paine *et al*., 2009). Different functional groups also differ in their responses to water stress. Thus, we postulate that the shift towards higher percentages of vines found in our study hectare is an indication for a shift to more generalist species that have better survival chances and are tolerant of varying hydric conditions rather then occupying only small ecological niches as most Amazonian tree species (Nascimento *et al*., 2005).

In the future, the importance of wider tolerance and response spectra for species survival may increase. If to date the high species diversity in Amazonian forests is related to a high specialization and niche compartmentalization (Walker, 1987), in the future these specialist species may be the losers and give way to generalist opportunistic species that can colonize sites with constantly changing water stress conditions. Amazonian floodplain forests may give us hope, because there hydric stress for trees is a recurrent phenomenon – in both terms of water excess and shortage (Parolin, 2001; Parolin *et al*., 2010), and yet these forests maintain a very high diversity of species (Wittmann *et al*., 2006) and functional groups. This indicates that extreme drought events will not necessarily drain all tree life forms from the existing forest. However, overall diversity will be reduced within very short time spans, with all the consequences for the ecosystem equilibrium and carbon balances which exert a strong worldwide influence (Soares-Filho *et al*., 2006; Phillips *et al*., 2009).

It is not a question whether hydric changes will occur that affect lowland forests. They always have occurred in form of *El Niño*-ENSO events, e.g. in the years 1983, 1992, 1997, 1998, and 2003 precipitation was only slightly above 1,500 mm as compared to 2,000 mm in normal years. And, as we know, they are strongly increasing in frequency and severity (Da Costa *et al.*, 2009). However, for the scientific community the question is how the forests will respond to increasing hydric stress events. As the results of our study indicate, we must expect strong shifts of species and functional groups after only a few years. Few species present the necessary adaptations to tolerate a wide range of hydric conditions, and only these have a chance of survival.

Changes in land use, such as urbanization, cultivation, and pastures, have been generally considered to be one of the main factors impacting Amazonian biodiversity. However, the impacts related to climatic changes are far more worrying, especially because its effects on biodiversity are still little studied. The Amazon region can be categorized as a region of great risk because of its social and climatic variability, and the synergic interactions of disordered processes of occupation of the region, leading to deforestation and land use changes. Models indicate the possibility of abrupt and irreversible substitutions of forested areas with open vegetation formations with less biomass, large-scale losses of biodiversity and reductions of the supporting capacity of the region (Nobre *et al*., 2007).

The loss of species richness and diversity in an Amazonian tropical forests, shown in the present study as a result of artificially simulating drought *El Niño* events, gives us clear signals that it is necessary to propose strategies for minimizing the climatic impact of changes at global scale

ACKNOWLEDGEMENTS

The authors thank Plinio Camargo and Scott Saleska for the invitation to participate in the course International Research and Education Project (PIRE). Thanks are also given to the technical coordinator of the Scientific Station Ferreira Penna, Mrs. Rosa Paes, for her help during our stay at the field station, and to Luiz Carlos Batista Lobato, for help during data collection and with species identification.

REFERENCES

AKCAKAYA, H., D. KEITH, W. THUILLER, G. MIDGLEY, R. PEARSON, S. PHILLIPS, H. M. REGAN, M. B. ARAÚJO & T. REBELO, 2008. Predicting extinction risks under climate change: integrating stochastic metapopulation models with dynamic bioclimatic habitat models. **Annual Meeting of the International Congress for Conservation Biology**. Available at: <http://www.allacademic.com/meta/p240064_index.html>. Accessed on: 9 Junho 2017.

ALENCAR, A. A. C., L. A. SOLORZANO & D. C. NEPSTAD, 2004. Modeling forest understory fires in an eastern Amazonian landscape. **Ecological Applications** 14(sp4): 139-149. DOI: http://dx.doi.org/10.1890/01-6029.

ALMEIDA, S. S., P. L. B. LISBOA & A. S. L. SILVA, 1993. Diversidade florística de uma comunidade arbórea na Estação Científica "Ferreira Penna", em Caxiuanã (Pará). **Boletim do Museu Paraense Emílio Goeldi. Série Botânica** 9: 99-128.

ANDERSON, M. J., 2001. A new method for non-parametric multivariate analysis of variance. **Austral Ecology** 26(1): 32-46.

ASNER, G. P., T. K. RUDEL & T. M. AIDE, 2009. A contemporary assessment of change in humid tropical forests. **Conservation Biology** 23(6): 1386-1395. DOI: http://dx.doi.org/10.1111/j.1523-1739.2009.01333.x.

BARLOW, J. & C. A. PERES, 2004. Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. **Philosophical Transactions of the Royal Society B** 359(1443): 367-380. DOI: http://dx.doi.org/10.1098/rstb.2003.1423.

BARLOW, J. & C. A. PERES, 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. **Philosophical Transactions ot the Royal Society B** 363(1498): 1787-1794. DOI: http://dx.doi.org/10.1098/rstb.2007.0013.

BORCHERT, R., G. RIVERA & W. HAGNAUER, 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. **Biotropica** 34(1): 27-39. DOI: http://dx.doi.org/10.1111/j.1744-7429.2002.tb00239.x.

BUNKER, D. E. & W. P. CARSON, 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. **Journal of Ecology** 93(4): 794-806. DOI: http://dx.doi.org/10.1111/j.1365-2745.2005.01019.x.

CAI, Z.-Q., S. A. SCHNITZER & F. BONGERS, 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. **Oecologia** 161(1): 25-33. DOI: http://dx.doi.org/10.1007/s00442-009-1355-4.

CLARK, D. A., 2007. Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. **Biotropica** 39(1): 4-19. DOI: http://dx.doi.org/10.1111/j.1744-7429.2006.00227.x.

COCHRANE, M. A. & C. P. BARBER, 2009. Climate change, human land use and future fires in the Amazon. **Global Change Biology** 15(3): 601-612. DOI: http://dx.doi.org/10.1111/j.1365-2486.2008.01786.x.

CONDIT, R., S. P. HUBBELL & R. B. FOSTER, 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. **Ecological Monographs** 65(4): 419-439. DOI: http://dx.doi.org/10.2307/2963497.

CONDIT, R., S. P. HUBBELL & R. B. FOSTER, 1996. Assessing the response of plant functional types to climatic change in tropical forests. **Journal of Vegetation Science** 7(3): 405-416. DOI: http://dx.doi.org/10.2307/3236284.

DA COSTA, A. C. L., 2008. **Projeto ESECAFLOR (Estudo da Seca da Floresta)**: Relatório Final: 1-68. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Belém.

DA COSTA, A. C. L., S. S. ALMEIDA, C. R. CARVALHO, P. MEIR, Y. MALHI, R. F. COSTA, J. A. S. JÚNIOR, M. C. COSTA, B. T. TANAKA, R. A. FISHER, E. D. SOTTA, L. L. OLIVEIRA, P. H. L. GONÇALVES, A. P. BRAGA & P. N. BARRETO, 2009. Experimento ESECAFLOR-LBA em Caxiuanã. In: P. L. B. LISBOA (Ed.): **Caxiuanã**: desafios para a conservação de uma Floresta Nacional na Amazônia: 45-97. Museu Paraense Emílio Goeldi, Belém.

ENGELBRECHT, B. M. J., S. J. WRIGHT & D. DE STEVEN, 2002. Survival and ecophysiology of tree seedlings during El Ninõ drought in a tropical moist forest in Panama. **Journal of Tropical Ecology** 18(4): 569-579. DOI: https://doi.org/10.1017/S0266467402002377.

ENGELBRECHT, B. M. J., L. S. COMITA, R. CONDIT, T. A. KURSAR, M. T. TYREE, B. L. TURNER & S. P. HUBBELL, 2007. Drought sensitivity shapes species distribution patterns in tropical forests. **Nature** 447: 80-82. DOI: http://dx.doi.org/10.1038/nature05747.

FERREIRA, L. V., S. S. ALMEIDA, D. D. AMARAL & P. PAROLIN, 2005. Riqueza e composição de espécies da floresta de igapó e várzea da Estação Científica Ferreira Penna: subsídios para o plano de manejo da Floresta Nacional de Caxiuanã. **Pesquisas, Botânica** 56: 103-116.

GUARIGUATA, M. R., J. P. CORNELIUS, B. LOCATELLI, C. FORNER & G. A. SÁNCHEZ-AZOFEIFA, 2008. Mitigation needs adaptation: tropical forestry and climate change. **Mitigation and Adaptation Strategies for Global Change** 13(8): 793-808

LAURANCE, W. F. & G. B. WILLIAMSON, 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. **Conservation Biology** 15(6): 1529-1535. DOI: http://dx.doi.org/10.1046/j.1523-1739.2001.01093.x.

LAURANCE, W. F., M. A. COCHRANE, S. BERGEN, P. M. FEARNSIDE, P. DELAMÔNICA, C. BARBER, S. D'ANGELO & T. FERNANDES, 2001. Environment: the future of the Brazilian Amazon. **Science** 291(5503): 438-439. DOI: http://dx.doi.org/10.1126/science.291.5503.438.

LAURANCE, W. F., G. POWELL & L. HANSEN, 2002. A precarious future for Amazonia. **Trends in Ecology & Evolution** 17(6): 251-252. DOI: http://dx.doi.org/10.1016/S0169-5347(02)02484-9.

MARENGO, J. A., C. A. NOBRE, J. TOMASELLA, M. D. OYAMA, G. SAMPAIO DE OLIVEIRA, R. OLIVEIRA, H. CAMARGO, L. M. ALVES & I. F. BROWN, 2008. The drought of Amazonia in 2005. **Journal of Climate** 21(3): 495-516. DOI: https://doi.org/10.1175/2007JCLI1600.1.

MCDOWELL, N., W. T. POCKMAN, C. D. ALLEN, D. D. BRESHEARS, N. COBB, T. KOLB, J. PLAUT, J. SPERRY, A. WEST, D. G. WILLIAMS & E. A. YEPEZ, 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? **New Phytologist** 178(4): 719-739. DOI: https://doi.org/10.1111/j.1469-8137.2008.02436.x.

NASCIMENTO, H. E. M., W. F. LAURANCE, R. CONDIT, S. G. LAURANCE, S. D'ANGELO & A. C. ANDRADE, 2005. Demographic and life-history correlates for Amazonian trees. **Journal of Vegetation Science** 16(6): 625-634. DOI: http://dx.doi.org/10.1111/j.1654-1103.2005.tb02405.x.

NEPSTAD, D. C., I. M. TOHVER, D. RAY, P. MOUTINHO & G. CARDINOT, 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. **Ecology** 88(9): 2259-2269. DOI: http://dx.doi.org/10.1890/06-1046.1.

NOBRE, A. C., G. SAMPAIO & L. SALAZAR, 2007. Mudanças climáticas e Amazônia. **Ciência e Cultura** 59(3): 22-27.

PAINE, C. E. T., K. E. HARMS & J. RAMOS, 2009. Supplemental irrigation increases seedling performance and diversity in a tropical forest. **Journal of Tropical Ecology** 25(2): 171-180. DOI: https://doi.org/10.1017/S0266467408005798.

PAROLIN, P., 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. **Oecologia** 128(3): 326-335. DOI: https://doi.org/10.1007/s004420100660.

PAROLIN, P., C. LUCAS, M. T. F. PIEDADE & F. WITTMANN, 2010. Drought responses of extremely flood-tolerant trees of Amazonian floodplains. **Annals of Botany** 105(1): 129-139. DOI: http://dx.doi.org/10.1093/aob/mcp258.

PHILLIPS, O. L., L. E. O. C. ARAGÃO, S. L. LEWIS, J. B. FISHER, J. L. LLOYD, G. LOPEZ-GONZALEZ, Y. MALHI, A. MONTEAGUDO, J. PEACOCK, C. A. QUESADA, G. VAN DER HEIJDEN, S. S. ALMEIDA, I. AMARAL, L. ARROYO, S. AYMARD, T. R. BAKER, O. BANKI, L. BLANC, D. BONAL, P. BRANDO, J. CHAVE, A. C. A. OLIVEIRA, N. D. CARDOZO, C. I. CZIMCZIK, T. R. FELDPAUSCH, M. A. FREITAS, E. GLOOR, N. HIGUCHI, E. JIMENEZ, G. LLOYD, P. MEIR, C. MENDOZA, A. MOREL, D. A. NEILL, D. NEPSTAD, S. PATINO, M. C. PENUELA, A. PRIETO, F. RAMIREZ, M. SCHWARZ, J. SILVA, M. SILVEIRA, A. S. THOMAS, H. TER STEEGE, J. STROPP, R. VASQUEZ, P. ZELAZOWSKI, E. A. DAVILA, S. ANDELMAN, A. ANDRADE, K. J. CHAO, T. ERWIN, A. DI FIORE, K. EHCH, T. J. KILLEEN, W. F. LAURANCE, A. P. CRUZ, N. C. A. PITMAN, P. N. VARGAS, H. RAMIREZ-ANGULO, A. RUDAS, R. SALOMÃO, N. SILVA, J. TERBORGH & A. TORRES-LEZAMA, 2009. Drought sensitivity of the Amazon rainforest. **Science** 323(5919): 1344-1347. DOI: http://dx.doi.org/10.1126/science.1164033.

POORTER, L. & L. MARKESTEIJN, 2008. Seedling traits determine drought tolerance of tropical tree species. **Biotropica** 40(3): 321-331. DOI: https://doi.org/10.1111/j.1744-7429.2007.00380.x.

RIGHI, C. A., P. M. L. D. GRAÇA & C. C. CERRI, 2009. Biomass burning in Brazil's Amazonian "arc of deforestation": burning efficiency and charcoal formation in a fire after mechanized clearing at Feliz Natal, Mato Grosso. **Forest Ecology and Management** 258(11): 2535-2546. DOI: https://doi.org/10.1016/j.foreco.2009.09.010.

SAIKI, S.-T., A. ISHIDA, K. YOSHIMURA & K. YAZAKI, 2017. Physiological mechanisms of drought-induced tree die-off in relation to carbon, hydraulic and respiratory stress in a drought-tolerant woody plant. **Scientific Reports** (2995): 1-10. DOI: http://dx.doi.org/10.1038/s41598-017-03162-5.

SOARES-FILHO, B. S., D. C. NEPSTAD, L. M. CURRAN, G. C. CERQUEIRA, R. A. GARCIA, C. A. RAMOS, E. VOLL, A. MCDONALD, P. LEFEBVRE & P. SCHLESINGER, 2006. Modelling conservation in the Amazon basin. **Nature** 440: 520-523. DOI: http://dx.doi.org/10.1038/nature04389.

STICKLER, C. M., D. C. NEPSTAD & M. T. COE, 2009. The potential ecological costs and cobenefits of REDD: a critical review and case study from the Amazon region. **Global Change Biology** 15(12): 2803-2824. DOI: http://dx.doi.org/10.1111/j.1365-2486.2009.02109.x.

STORK, N. E., J. A. CODDINGTON & R. K. COLWELL, 2009. Vulnerability and resilience of tropical forest species to land-use change. **Conservation Biology** 23(6): 1438-1447. DOI: http://dx.doi.org/10.1111/j.1523-1739.2009.01335.x.

TIMMERMAN, A., J. OBERHUBER, A. BACHER, M. ESCH, M. LATIF & E. ROECKNER, 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. **Nature** 398: 694-697. DOI: http://dx.doi.org/10.1038/19505.

WALKER, I., 1987. Compartmentalization and niche differentiation: causal patterns of competition and coexistence. **Acta Biotheoretica** 36(4): 215-239. DOI: http://dx.doi.org/10.1007/BF02329784.

WITTMANN, F., J. SCHÖNGART, J. C. MONTERO, T. MOTZER, W. J. JUNK, M. T. F. PIEDADE, H. L. QUEIROZ & M. WORBES, 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. **Journal of Biogeography** 33(8): 1334-1347. DOI: http://dx.doi.org/10.1111/j.1365-2699.2006.01495.x.

WRIGHT, S. J., O. CALDERÓN, A. HERNANDÉZ & S. PATON, 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. **Ecology** 85(2): 484-489. DOI: http://dx.doi.org/10.1890/02-0757.

ZAR, J. H., 2010. **Biostatistical analysis**: 5. ed.: 1-960. Prentice-Hall, Englewood Cliffs, New Jersey.

APPENDIX. List of species in decreasing density in the control (C) and experimental (E) plots of the ESECAFLOR Project. (Continue)

#	Species	Family	Life form	Plot C	Plot E	Total
1	*Pouteria cladantha* Sandwith	Sapotaceae	Arboreal	43	19	62
2	*Vouacapoua americana* Aubl.	Caesalpinaceae	Arboreal	44	15	59
3	*Lecythis idatimon* Aubl.	Lecythidaceae	Arboreal	34	21	55
4	*Faramea bracteata* Benth.	Rubiaceae	Shrubby	40	11	51
5	*Rinorea guianensis* Aubl.	Violaceae	Arboreal	31	8	39
6	*Doliocarpus dentatus* (Aubl.) Standl.	Dilleniaceae	Liana	20	12	32
7	*Memora flavida* (DC.) Bureau & K. Schum.	Bignoniaceae	Liana	11	19	30
8	*Inga alba* (Sw.) Willd.	Mimosaceae	Arboreal	17	11	28
9	*Protium apiculatum* Swart	Burseraceae	Arboreal	18	8	26
10	*Qualea paraensis* Ducke	Vochysiaceae	Arboreal	17	7	24
11	*Eugenia coffeifolia* DC.	Myrtaceae	Shrubby	8	14	22
12	*Duguetia echinophora* R.E. Fr.	Annonaceae	Arboreal	20	1	21
13	*Inga lateriflora* Miq.	Mimosaceae	Arboreal	9	12	21
14	*Protium pilosissimum* Engl.	Burseraceae	Arboreal	10	11	21
15	*Licania membranacea* Sagot ex Laness.	Chrysobalanaceae	Arboreal	13	7	20
16	*Cheiloclinium cognatum* (Miers) A.C. Sm.	Hippocrateaceae	Liana	8	10	18
17	*Licania canescens* Benoist	Chrysobalanaceae	Arboreal	13	5	18
18	*Monotagma floribundum* Hagberg & R. Erikss.	Marantaceae	Herbaceous	5	10	15
19	*Rinorea passoura* Kuntze	Violaceae	Arboreal	7	8	15
20	*Salacia impressifolia* (Miers) A.C. Sm.	Hippocrateaceae	Liana	7	8	15
21	*Psychotria racemosa* Rich.	Rubiaceae	Shrubby	4	10	14
22	*Mouriri callocarpa* Ducke	Melastomataceae	Arboreal	10	3	13
23	*Swartzia recurva* Poepp.	Fabaceae	Arboreal	6	6	12
24	*Memora schomburgkii* (DC.) Miers	Bignoniaceae	Liana	9	2	11
25	*Brosimum rubescens* Taub.	Moraceae	Arboreal	9	1	10
26	*Bauhinia guianensis* Aubl.	Caesalpinaceae	Liana	4	5	9
27	*Duguetia cadaverica* Huber	Annonaceae	Arboreal	7	2	9
28	*Moutabea guianensis* Aubl.	Polygalaceae	Liana	5	4	9
29	*Ouratea discophora* Ducke	Ochnaceae	Arboreal	4	5	9
30	*Astrocaryum aculeatum* G. Mey.	Arecacae	Arboreal	3	5	8
31	*Dinizia excels* Ducke	Mimosaceae	Arboreal	3	5	8
32	*Iryanthera laevis* Markgr.	Myristicaceae	Arboreal	8		8
33	*Minquartia guianensis* Aubl.	Olacaceae	Arboreal	6	2	8
34	*Monotagma acuminata*	Marantaceae	Herbaceous	6	2	8
35	*Protium tenuifolium* (Engl.) Engl.	Burseraceae	Arboreal	7	1	8
36	*Abuta sandwithiana* Krukoff & Barneby	Menispermaceae	Liana	5	2	7
37	*Aniba parviflora* (Meisn.) Mez	Lauraceae	Arboreal	4	3	7

APPENDIX. (Continue)

#	Species	Family	Life form	Plot C	Plot E	Total
38	*Connarus erianthus* Benth. ex Baker	Connaraceae	Liana	7		7
39	*Cordia nodosa* Lam.	Boraginaceae	Arboreal	4	2	6
40	*Eschweilera coriacea* (DC.) S.A. Mori	Lecythidaceae	Arboreal	6		6
41	*Paypayrola grandifolia* Tul.	Violaceae	Arboreal	2	4	6
42	*Pouteria anibiifolia* (A.C. Smith.) Aubr.	Sapotaceae	Arboreal	6		6
43	*Pouteria filipes* Eyma	Sapotaceae	Arboreal	4	2	6
44	*Protium subserratum* (Engl.) Engl.	Burseraceae	Arboreal	3	3	6
45	*Sloanea eichleri* K. Schum.	Elaeocarpaceae	Arboreal	4	2	6
46	*Virola michelii* Heckel	Myristicaceae	Arboreal	4	2	6
47	*Aspidosperma nitidum* Benth. ex Müll. Arg.	Apocynaceae	Arboreal	5		5
48	*Ischnosiphon arouma* (Aubl.) Körn.	Marantaceae	Herbaceous	5		5
49	*Micropholis venulosa* (Mart. & Eichler) Pierre	Sapotaceae	Arboreal	5		5
50	*Ocotea canaliculata* (Rich.) Mez	Lauraceae	Arboreal	4	1	5
51	*Pouteria decorticans* T.D. Penn.	Sapotaceae	Arboreal	4	1	5
52	*Prionostemma asperum* (Lam.) Miers	Hippocrateaceae	Liana		5	5
53	*Protium decandrum* (Aubl.) Marchand	Burseraceae	Arboreal	4	1	5
54	*Psychotria colorata* (Willd. ex Roem. & Schult.) Müll. Arg.	Rubiaceae	Shrubby	2	3	5
55	*Astronium gracile* Engl.	Anacardiaceae	Arboreal	3	1	4
56	*Derris floribunda* (Benth.) Ducke	Fabaceae	Liana	4		4
57	*Eugenia cupulata* Amshoff	Myrtaceae	Arboreal		4	4
58	*Hymenolobium petraeum* Ducke	Leg_Papilionoidae	Arboreal	4		4
59	*Inga gracilis* Jungh. ex Miq.	Mimosaceae	Arboreal	2	2	4
60	*Ocotea caudate* (Nees) Mez	Lauraceae	Arboreal	1	3	4
61	*Protium spruceanum* (Benth.) Engl.	Burseraceae	Arboreal	4		4
62	*Strychnos amazonica* Krukoff	Loganiaceae	Liana	4		4
63	*Stryphnodendron paniculatum* Poepp.	Mimosaceae	Arboreal	4		4
64	*Astrocaryum gynacanthum* Mart.	Arecacae	Arboreal	2	1	3
65	*Erythroxylum micranthum* Bong. ex Peyr.	Erythroxylaceae	Shrubby	2	1	3
66	*Geonoma bacculifera* (Poit.) Kunth	Arecacae	Shrubby	1	2	3
67	*Manilkara huberi* (Ducke) A. Chev.	Sapotaceae	Arboreal	2	1	3
68	*Miconia splendens* (Sw.) Griseb.	Melastomataceae	Arboreal	2	1	3
69	*Parinari excels* Sabine	Chrysobalanaceae	Arboreal	2	1	3
70	*Pouteria guianensis* Aubl.	Sapotaceae	Arboreal	3		3
71	*Psychotria poeppigiana* Müll. Arg.	Rubiaceae	Shrubby	2	1	3
72	*Swartzia arborescens* (Aubl.) Pittier	Fabaceae	Arboreal	3		3
73	*Trichilia micrantha* Benth.	Meliaceae	Arboreal		3	3
74	*Anacampta flavencens*	Apocynaceae	Shrubby	2		2

APPENDIX. (Continue)

#	Species	Family	Life form	Plot C	Plot E	Total
75	*Arrabidaea cinnamomea* (DC.) Sandwith	Bignoniaceae	Liana	2		2
76	*Banisteriopsis lucida* (Rich.) Small	Malpighiaceae	Liana		2	2
77	*Couratari guianensis* Aubl.	Lecythidaceae	Arboreal	2		2
78	*Endlicheria bracteata* Mez	Lauraceae	Arboreal	1	1	2
79	*Guarea kunthiana* A. Juss.	Meliaceae	Arboreal	2		2
80	*Helicostylis pedunculata* Benoist	Moraceae	Arboreal		2	2
81	*Heliconia psittacorum* L. f.	Heliconiaceae	Herbaceous	1	1	2
82	*Hirtella racemosa* Lam.	Chrysobalanaceae	Shrubby	1	1	2
83	*Inga macrophylla* Humb. & Bonpl. ex Willd.	Mimosaceae	Arboreal		2	2
84	*Inga stipularis* DC.	Mimosaceae	Arboreal	2		2
85	*Iryanthera paraensis* Huber	Myristicaceae	Arboreal	2		2
86	*Lacunaria crenata* (Tul.) A.C. Sm.	Quiinaceae	Arboreal	2		2
87	*Licania apetala* (E. Mey.) Fritsch	Chrysobalanaceae	Arboreal	2		2
88	*Maquira sclerophylla* (Ducke) C.C. Berg	Moraceae	Arboreal	2		2
89	*Memora allamandiflora* Bureau ex K. Schum.	Bignoniaceae	Liana		2	2
90	*Moronobea coccinea* Aubl.	Clusiaceae	Arboreal	2		2
91	*Pouteria eugeniifolia* (Pierre) Baehni	Sapotaceae	Arboreal	1	1	2
92	*Protium paniculatum* Engl.	Burseraceae	Arboreal		2	2
93	*Protium sagotianum* Marchand	Burseraceae	Arboreal	2		2
94	*Quiina florida* Tul.	Quiinaceae	Arboreal	1	1	2
95	*Scyatodenia* sp.	Menispermaceae	Liana		2	2
96	*Tetracera wildenowiana*	Dilleniaceae	Liana	2		2
97	*Unonopsis guatterioides* (A. DC.) R.E. Fr.	Annonaceae	Arboreal	1	1	2
98	*Vantanea parviflora* Lam.	Humiriaceae	Arboreal		2	2
99	*Virola calophylla* (Spruce) Warb.	Myristicaceae	Arboreal	1	1	2
100	*Acacia multipinnata* Ducke	Mimosaceae	Liana		1	1
101	*Alchornea schomburgkii* Klotzsch	Euphorbiaceae	Arboreal		1	1
102	*Alchorneopsis floribunda* (Benth.) Müll. Arg.	Euphorbiaceae	Arboreal	1		1
103	*Allophylus divaricatus* Radlk.	Sapindaceae	Arboreal	1		1
104	*Anaxagorea amazonica*	Annonaceae	Arboreal	1		1
105	*Arrabidaea bilabiata* (Sprague) Sandwith	Bignoniaceae	Liana	1		1
106	*Aspidosperma auriculatum* Markgr.	Apocynaceae	Arboreal		1	1
107	*Brosimum guianense* (Aubl.) Huber	Moraceae	Arboreal	1		1
108	*Caryocar glabrum* (Aubl.) Pers.	Caryocaraceae	Arboreal	1		1
109	*Casearia decandra* Jacq.	Flacourtiaceae	Arboreal		1	1
110	*Cissampelus* sp.	Menispermaceae	Liana	1		1
111	*Couma guianensis* Aubl.	Apocynaceae	Arboreal		1	1

APPENDIX. (Continue)

#	Species	Family	Life form	Plot C	Plot E	Total
112	*Dioclea bicolor* Benth.	Fabaceae	Liana	1		1
113	*Diospyros praetermissa* Sandwith	Ebenaceae	Arboreal	1		1
114	*Ecclinusa ramiflora* Mart.	Sapotaceae	Arboreal		1	1
115	*Eugenia flavescens* DC.	Myrtaceae	Shrubby	1		1
116	*Guatteria olivacea* R.E. Fr.	Annonaceae	Arboreal	1		1
117	*Hippocratea ovate* Lam.	Hippocrateaceae	Liana	1		1
118	*Inga brachyrhachys*	Mimosaceae	Shrubby	1		1
119	*Inga grandifolia* Pittier	Mimosaceae	Arboreal	1		1
120	*Inga marginata* Willd.	Mimosaceae	Arboreal	1		1
121	*Inga nobilis* Willd.	Mimosaceae	Arboreal	1		1
122	*Inga rubiginosa* (Rich.) DC.	Mimosaceae	Arboreal	1		1
123	*Lacunaria jenmanii* (Oliv.) Ducke	Quiinaceae	Arboreal		1	1
124	*Licania gracilis* Kleinhoonte	Chrysobalanaceae	Arboreal		1	1
125	*Maquina caloneura*	Moraceae	Arboreal		1	1
126	*Matayba arborescens* (Aubl.) Radlk.	Sapindaceae	Arboreal	1		1
127	*Miconia ciliate* (Rich.) DC.	Melastomataceae	Shrubby	1		1
128	*Miconia holosericea* (L.) DC.	Melastomataceae	Shrubby	1		1
129	*Myrcia fallax* (Rich.) DC.	Myrtaceae	Arboreal	1		1
130	*Myrcia sylvatica* (G. Mey.) DC.	Myrtaceae	Arboreal		1	1
131	*Ocotea cujumary* Mart.	Lauraceae	Arboreal		1	1
132	*Palicourea* sp.	Rubiaceae	Shrubby	1		1
133	*Potalia amara* Aubl.	Loganiaceae	Shrubby	1		1
134	*Pouteria campanulata* Baehni	Sapotaceae	Arboreal	1		1
135	*Pouteria gongrijpii* Eyma	Sapotaceae	Arboreal	1		1
136	*Pouteria robusta* (Mart. & Eichler) Eyma	Sapotaceae	Arboreal	1		1
137	*Protium guianense* (Aubl.) Marchand	Burseraceae	Arboreal	1		1
138	*Guarea kunthiana* A. Juss.	Meliaceae	Arboreal	1		1
139	*Saccoglotis guianensis* Benth.	Humiriaceae	Arboreal	1		1
140	*Sagotia brachysepala* (Müll. Arg.) Secco	Euphorbiaceae	Shrubby	1		1
141	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae	Arboreal	1		1
142	*Senefeldera macrophylla* Ducke	Euphorbiaceae	Arboreal	1		1
143	*Siparuna amazonica* Mart. ex A. DC.	Monimiaceae	Arboreal	1		1
144	*Smilax schomburgkiana* Kunth	Smilacaceae	Liana		1	1
145	*Sterculia pruriens* (Aubl.) K. Schum.	Sterculiaceae	Arboreal	1		1
146	*Swartzia ferruginea*	Fabaceae	Arboreal	1		1
147	*Tabernaemontana angulate* Mart. ex Müll. Arg.	Apocynaceae	Shrubby	1		1
148	*Tachigali paniculata* Aubl.	Caesalpinaceae	Arboreal		1	1

APPENDIX. (Conclusion)

#	Species	Family	Life form	Plot C	Plot E	Total
149	*Tovomita brevistaminea* Engl.	Clusiaceae	Arboreal	1		1
150	*Trichilia quadrijuga* Kunth	Meliaceae	Arboreal	1		1
151	*Xylopia nitida* Dunal	Annonaceae	Arboreal	1		1
152	*Zygia racemosa* (Ducke) Barneby & J.W. Grimes	Mimosaceae	Arboreal	1		1