



Aboveground Biomass Dynamics in the Amazonian Rainforest under Influence of Reduction in Rainfall

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Abstract

Exchange of biomass between the ecosystem and the atmosphere plays an important role in regional and global carbon cycles that have a major impact on biodiversity. This study evaluated the effect of reduction in rainfall on the aboveground biomass in an Amazonian rainforest. Data for this study were obtained from the “Long-term drought impact on water and carbon dioxide fluxes in Amazonian Tropical Rainforest Experiment (ESECAFLOR)” which was a subproject of Large Scale Biosphere Atmosphere Experiment in Amazon forest (LBA), carried out in *terra firma* rainforest in Caxiuana National Forest, Pará, Brazil. The experimental design entailed two experimental sites each with one hectare of natural forest: control TFE (a simulated soil drought or ‘throughfall exclusion’ experiment) under normal conditions of climate and treatment TFE with rainfall exclusion of about 50%. The tree growth parameters employed in the study were based on monthly data from the experimental period from January 2005 to May 2009. Results indicated that a decrease in rainfall significantly affected the tree growth parameters, resulting in a decrease of biomass ($21.1 \text{ t ha}^{-1} \text{ year}^{-1}$) and basal area ($1.04 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$). The Amazonian rainforest may become increasingly vulnerable to higher background tree mortality rates in response to drought events, such as El Niño.

Keyword: Basal area, Biomass increment, Caxiuana reserve, Tree mortality

Introduction

Recent analyses suggest that carbon dynamics of the Amazonian tropical forests vary interannually in response to rainfall and temperature anomalies [1]. Using simulated soil-moisture droughts or TFE experiments (throughfall exclusion experiment), effects of severe droughts as a consequence of climate change, have been investigated in the eastern Amazonian rainforest. These investigations have analyzed tropical forests which have been subjected to increasingly severe drought episodes through the El-Niño/Southern Oscillation (ENSO). Davidson et al [2] studied the effect of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in Tapajós forest, Brazil. Using the same design as for the Caxiuana forest, Fisher et al [1] analyzed the response of an eastern Amazonian rainforest to drought stress using data from the TFE experiments. Both investigations were carried out as part of LBA, using two 100 m x100 m plots, one control plot and one treatment ‘TFE’ plot.

The aboveground biomass in tropical forests is mainly contained in trees. The tree biomass is a function of wood volume, obtained from the tree diameter and height, architecture and wood density. It can be quantified by a direct or an indirect method, where the biomass is quantified using a mathematical model. An allometric model can be site specific when elaborated to a particular ecosystem or can be general when used at different sites. Nogueira et al [3] presented biomass equations developed from trees directly weighed in open forest on fertile soils in the southern Amazon and allometric equations for bole-volume estimates of trees in both dense and open forests. These equations were used to improve the commonly used biomass models based on large-scale wood-volume inventories carried out in the Amazonian forest. However, estimates of biomass storage are discordant when the same method is applied or when estimates from allometric equations are compared with the biomass obtained from large-scale wood-volume inventories [4]. Also, there are difficulties

in accurately measuring the total or even merchantable tree height of tropical trees. Therefore, the diameter at breast height (DBH) has become the most important variable for allometric equations [5]. Also, the diameter increment measurements have been used to examine the dynamics of natural forests [6].

The tropical forests in Amazon and elsewhere are subjected to increasingly severe droughts as a consequence of climate change which seems to cause severe reductions in rainfall and other ecological functions. However, reduced rainfall on forest gives rise to major uncertainties as regards the future climate and their consequences are still not well understood. On the other hand, the fundamental mechanisms underlying tree survival and mortality during droughts remain less than well understood. Mortality of canopy trees is an important process in forest dynamics, and can be sudden, with no relationship to past events or the culmination of a long decline [7]. Some studies have included an extensive tree mortality of *Austrocedrus chilensis* during the El-Niño droughts in Argentina [8], and die-off of multiple pine species during the 1950s drought in the southwestern USA [9].

Using throughfall exclusion experiments in the Amazonian

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rainforest, Fisher et al [1] and Costa et al [10] investigated forest transpiration by the sap flow method in the Caxiuanã National Forest. Fisher et al [1] concluded that the forest was not able to withstand a 50% reduction in rainfall over 1-2 years without impacting the canopy gas exchange, while Costa et al [10] found a decrease of 68% in the mean transpiration of *E. Coriacea* from the control plot to the rainfall exclusion plot. Rainforests are forests characterized by high rainfall. However, the link between reduced rainfall and the aboveground biomass dynamics is poorly understood. Thus, it is important to know how the forest responds to drier soil conditions than those concurrently experienced in the control plot. The objective of this study, therefore, was to establish a throughfall exclusion experiment and analyze the biomass dynamics in the Amazonian rainforest under the influence of large reduction in rainfall, by excluding about 50% of rainwater from the soil for a long period (mimicking an extreme El-Niño).

Materials and Methods

Experimental site

This study was carried out at Ferreira Penna Scientific Station (FPSS) in the Caxiuanã National Forest (CNF) in Pará State (Latitude: 1°42'30"S, Longitude: 51°31'45"W and Altitude: 62 m above sea level), Brazil. The FPSS is located in the 300 000 hectare Caxiuanã National Forest, about 400 km to the west of Pará capital city of Belém, Brazil. The region has a well-preserved forest with a canopy of 35 m high. The Amazon is covered predominantly by moist dense tropical forest, but with several other vegetation types, including savannas, montane forests, open forests, floodplain forests, grasslands, swamps, bamboos, and palm forests [10]. Figure 1 shows the localization of FPSS in Pará State.

The predominant trees species in the landscape are *Eschweilera carinata* (Matamata), *Voucapoua americana* (Acapu), *Protium paraense* (Latilla), *Dinizia excelsa* (angelim-vermelho), *Marmaroxylon racemosum* (Marblewood), *Couratari guianensis* (Mahot), *Buchenavia capitata* (Yellow Sanders), *Swartzia racemosa* (pitaica), and *Dipteryx odorata* (Sarrapia). The forest is a lowland *terra firme* rainforest. The mean annual temperature is 25.78°C and the mean annual rainfall is 2272 mm, with a dry season when only 555 mm of rainfall occurs on average [1]. The wet season is from January to June, while the dry season is from July to December. Most soils are yellow Oxisols (Brazilian classification Latossolo), but there are large differences in texture. The water table has been observed at a soil depth of 10 m during the wet season and the site elevation is 15 m above the river level [1].

ESECAFLOR experiment

The data used in this study were obtained from the "Long-term drought impact on water and carbon dioxide fluxes in Amazonian Tropical Rainforest Experiment" (ESECAFLOR) which was a subproject of Large Scale Biosphere Atmosphere Experiment in Amazon forest (LBA). The ESECAFLOR experiment compared water and carbon dioxide fluxes over the tropical rainforest ecosystem with those of an experimental plot in which rainfall was artificially excluded (about 50%) to simulate a severe drought in eastern Amazon which was associated with the El-Niño years. A "throughfall" exclusion (TFE) experiment was conducted at the experimental site where rainfall was excluded from the soil over a 100 m x 100 m plot (treatment) and the data were compared to those concurrently experienced in another 100 m x 100 m plot (control). Further details about the "TFE" experiment in eastern Amazon are provided in Fisher et al [1]. Our study analyzed observations of biomass dynamics from January 2005 to May 2009, and the observations were not replicated.

Description of data

Field measurements were performed on Plot A (control TFE) and Plot B (treatment TFE) in which rainfall was artificially excluded to simulate a drought as previously mentioned. Based on at least one stem with a diameter at the breast height (DBH) > 5 cm, the number of trees were 532 and 502 for control TFE and treatment TFE, respectively. The most predominant tree species in control TFE were *Eschweilera odorata* (Siam Weed), *Lecythis lanceolata* (sapucaia-mirim), *Licania octandra* (Caraipé), *Pouteria macrophylla* (abiu), *Swartzia racemosa* (Pacapeuá), *Rinoria guianensis* (acariquarana) and *Voucapoua Americana* (Bruinhart). On the other hand, the tree species in the treatment TFE included *Eschweilera coriacea* (matamata), *Manilkara huberi* (Macaranduba), *Swartzia polyphylla* (Paracutaca) and *Tetragastris panamensis* (Amesclao).

The forest tree species diversity varied from 150 to 160 trees per hectare and the individual density ranged from 450 to 550 trees ha⁻¹. Each plot of 100 m x 100 m (1 ha) was divided into 100 subplots each 10 m x 10 m including different species. Metal dendrometer bands were fixed to the trunk of each selected tree for measuring changes in stem diameter through the return spring displacement. Displacement measurements were taken by a digital caliper with a precision of 0.01 mm. Since DBH measurements are important for assessing the biomass dynamics of tropical forest growth, the basal area was obtained by summing cross-sections of trees for a range of three classes of DBH.

As no allometric equations have been developed for old-growth Atlantic forest sites encompassing a range of tree diameters suitable for this study, we applied the allometric equations developed by Higuchi et al [11]. The tree aboveground biomass through experimental period was grouped into three diameter classes, defined as the largest (DBH ≥ 20 cm), the smallest (5 ≤ DBH < 20 cm) and unique class (DBH > 5 cm), as follows:

$$\ln P = -0.151 + 2.170 \ln \text{DBH}, \text{ for DBH} \geq 20 \text{ cm} \quad (1)$$

$$\ln P = -1.754 + 2.665 \ln \text{DBH}, \text{ for } 5 \leq \text{DBH} < 20 \text{ cm} \quad (2)$$

$$\ln P = -1.497 + 2.548 \ln \text{DBH}, \text{ for DBH} > 5 \text{ cm} \quad (3)$$

where, DBH is the diameter at the breast height (cm), and P is the total fresh weight (kg). These equations were derived by four statistical models from the data set with 315 trees with DBH greater than 5 cm on a site covered by a typical dense *terra firme* in Central Amazon. Higuchi et al [11] found that the logarithmic model using a single independent variable (DBH) produced results as consistent and precise as those with two variables (DBH and total height), with the differences between observed and estimated biomass being below 5%. In order to evaluate the forest structure and biomass variation under rainfall exclusion

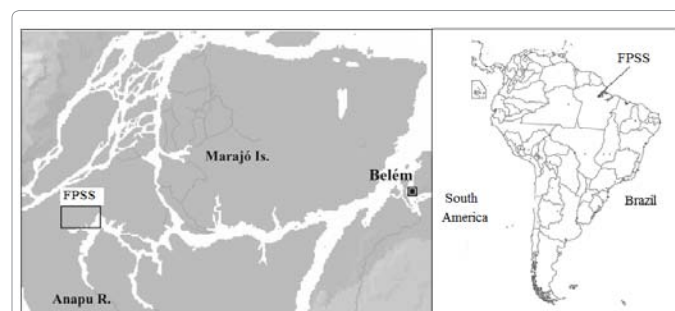


Figure 1: Location of Ferreira Penna Scientific Station (FPSS), in Caxiuanã, west de Belém and Marajó island, in Pará state, Brazil.

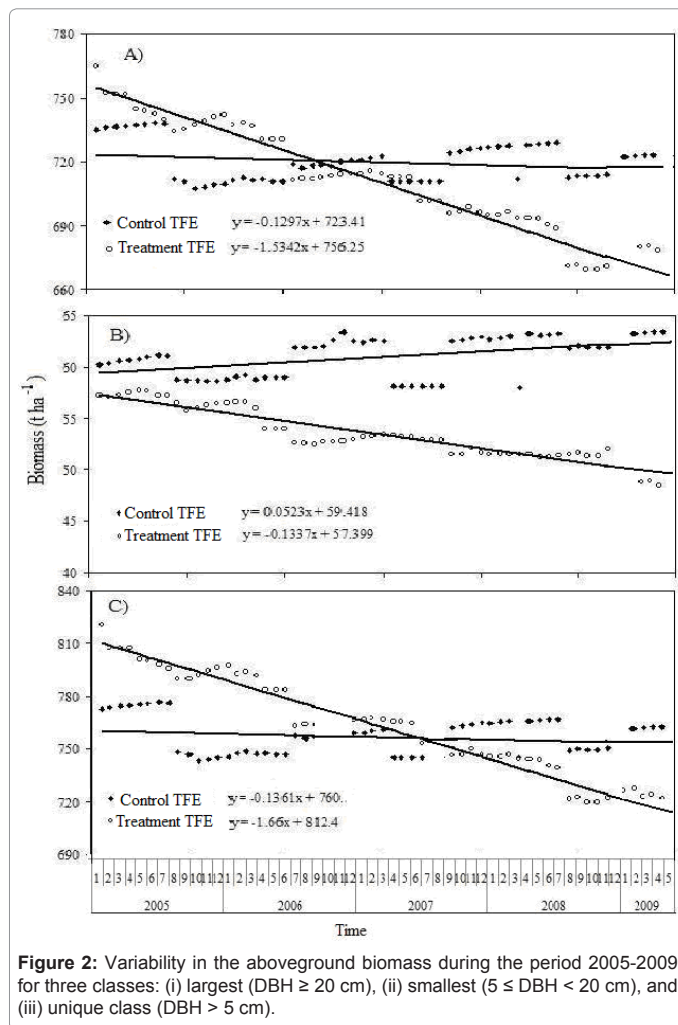


Figure 2: Variability in the aboveground biomass during the period 2005-2009 for three classes: (i) largest (DBH ≥ 20 cm), (ii) smallest (5 ≤ DBH < 20 cm), and (iii) unique class (DBH > 5 cm).

in our study, the biomass data were collected for the two plots from January 2005 to May 2009. The allometric equations relating diameter at the breast height to stem were derived from destructive sampling. The tree DBH and diameter measurements were made monthly on living trees in both plots.

Results

Biomass data and basal area

There was an appreciable difference in the aboveground biomass between control and treatment plots for all tree diameter classes throughout the study period, as shown in Figure 2, because rainfall was artificially excluded to simulate a severe drought which is associated with the El-Niño years. The aboveground biomass on control TFE did not practically vary during the experimental period, except for the smallest class with an increase of only 2.7 t ha⁻¹, while the other classes showed a little sign of decreasing trend. The biomass values declined from 755 to 670 t ha⁻¹ for the largest class, from 57 to 52 t ha⁻¹ for the smallest class and from 815 to 715 for the unique class.

While the forest biomass for the smallest class in control TFE increased with values ranging from 58 to 63 t ha⁻¹, the aboveground biomass in treatment TFE decreased from 57 to 52 t ha⁻¹. This result is particularly important, because the role of environmental variables that control the distribution and abundance of biomass in tropical lowland

forests has been a key property of ecosystems. In addition, forests can play an important role, since they can supply biomass residues that may constitute an important source of energy. Baker et al [12] discussed that uncertainty in biomass estimates is one of the greatest limitations of models of carbon flux in tropical forests.

The average basal area in control TFE was 32.3±0.45 (range 32.9 - 31.9 m² ha⁻¹); while in treatment TFE it was 30.8±1.41 (range 32.8 - 28.7 m² ha⁻¹). The highest difference between basal areas occurred at the end of the experimental period; the whole difference was up to 9%. There was a significant decrease in the basal area of 1.04 m² ha⁻¹ year⁻¹ in treatment TFE and almost no change in control TFE with an increase of only 0.11 m² ha⁻¹ year⁻¹, because rainfall did not practically vary from 2006-2009 (Table 1). However, in 2005, the biomass was lower than the average from 2005-2008 (755.7 t ha⁻¹), because rainfall was 50.3% lower than the long term mean (2272 mm). This rainfall decrease in 2005 was influenced by a strong El-Niño weather pattern producing droughts in the region and had amplified the annual rate of tree mortality in tropical forests of Brazil. It is important to highlight the fact that the aboveground biomass data in 2009 was not for the entire year (January-May).

Trees mortality

The losses of biomass through mortality under normal climate and drought events are shown in Figure 3. From the tree death data record (2005-2009), the loss of aboveground biomass through mortality was of 5.3 t ha⁻¹ year⁻¹ in control TFE and 21.1 t ha⁻¹ year⁻¹ in treatment TFE. Obviously, the average density (± standard deviation) of dead trees on treatment TFE was higher (54 ± 20.4 t ha⁻¹) than in control TFE (25.7 ± 7.1 t ha⁻¹) which can be attributed to a drought and heat stress.

Biomass (t ha ⁻¹)					
	2005	2006	2007	2008	2009
Control TFE					
Average	765	750	752	763	750
Standard deviation	4.9	14.6	7.5	5.9	0.6
Treatment TFE					
Average	800	782	763	745	721
Standard deviation	13.9	9.1	5.8	2.9	1.3
Rainfall (mm)					
Annual total	1143.0	2062.4	2079.8	2130.2	-
Standard deviation	123.7	137.7	122.7	168.5	-

Table 1: Annual rainfall, average, and standard deviation of the aboveground biomass for each year of the experimental period.

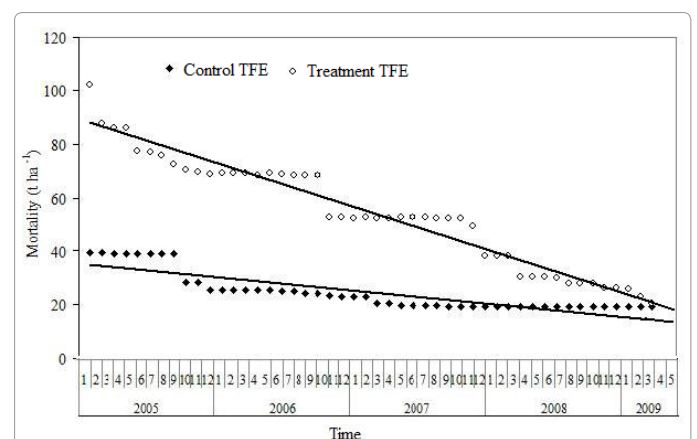


Figure 3: Temporal pattern of the loss of the aboveground biomass through mortality in control TFE and treatment TFE.

The frequency of tree death by year in control TFE and treatment TFE from 2005 to 2009 is shown in Figure 4. The frequency of tree deaths was averaged for a 1-year period for each plot. The temporal variation in the frequency of tree deaths was associated with droughts. In 2009, however, the tree deaths in the plot with rainfall exclusion were lower than those with normal climate, possibly due to the short record period (January to May) which was not representative for the entire year. Apart from that, due to rainfall exclusion, the frequency of trees that died was higher in treatment TFE than in control TFE, except in 2007, as a consequence of insects and disease activity on the plot under normal climate.

The mortality tree rate in treatment TFE was 3.7% year⁻¹ (ranging from 10 to 21 trees), whereas it was 2.6% year⁻¹ (ranging from 19 to 39 trees) in control TFE. Such values are similar to those obtained by Hu and Wang [13] who reported an annual tree mortality rate of 1.03±0.38% for South Carolina Piedmont. On the other hand, Laarmann et al [14] found an average annual tree mortality rate of 1.3% based on the initial stem numbers when analyzing forest naturalness and tree mortality patterns in Estonia. The biomass data was negatively correlated with the frequency of tree death in control TFE and treatment TFE (Figure 5). The decrease in the aboveground biomass in treatment TFE was explicated up to 97% by tree deaths as a consequence of reduced rainfall from January 2005 to May 2009. However, the tree mortality was not significantly correlated with biomass in control TFE, indicating that other factors, such as forest insects and disease activity, can be dominant to reduce the biomass [10]. The coefficient of determination of 0.9748 between biomass and tree mortality in treatment TFE is statistically significant at 1% level by the Student-t-test. However, there is not a statistically significant relationship between the variables for control TFE ($r^2 = 0.2481$).

Discussion

The seasonal pattern of tree density for three diameter classes in treatment TFE was essentially in decline, because rainfall was artificially excluded to simulate a severe drought in the forest. This result is particularly important, because extensive drought conditions experienced in eastern Amazon coincide with the El Niño/Southern Oscillation (ENSO) events. In addition, continued increase in the concentration of carbon dioxide in the atmosphere due to anthropogenic emissions is predicted to lead to significant changes in climate, especially in tropical rainforests, like the Amazon region. Analyzing the biomass and net primary productivity of forests in central Himalaya, India, Lodhiyal and Lodhiyal [15] observed that the basal area and biomass of trees increased with increase in the forest age,

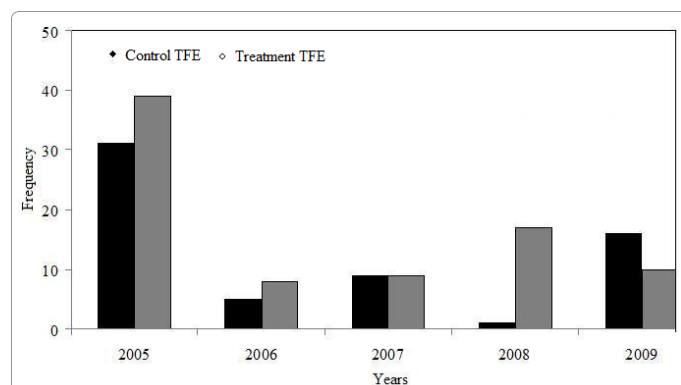


Figure 4: Frequency of tree death in control TFE and treatment TFE in Caxiuanã, Pará, Brazil.

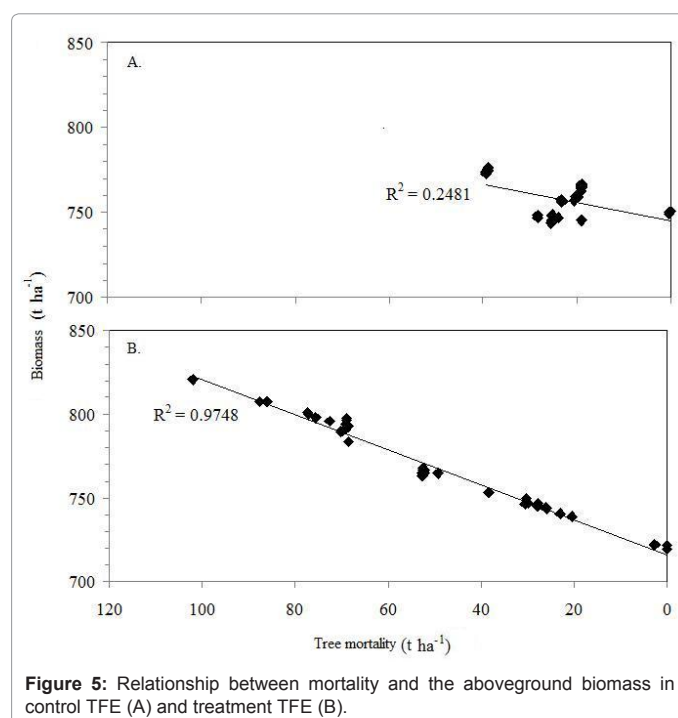


Figure 5: Relationship between mortality and the aboveground biomass in control TFE (A) and treatment TFE (B).

whereas the herb biomass significantly decreased with increasing forest age. They also found that the total vegetation biomass ranged from 52.5 (5 years) to 118.1 t ha⁻¹ (15 years).

The basal area decreased substantially and linearly in treatment TFE as a consequence of reduced soil water content produced by rainfall exclusion, while for the plot under normal conditions of climate the basal area was approximately constant (around 32.5 m² ha⁻¹) during the experimental period (Figure 6). Comparison of basal areas for two plots revealed no changes through the first year of experimental period, with the basal area in treatment TFE being higher than in control TFE. This difference was less than 1%, which can be explained by the fact that at the beginning of experiment the effect of drought in forest was not felt. However, the effect of drought impact became evident after 2005 because the basal was reduced by 12.5% at the end of experimental period in May 2009. Marín et al [16] found basal areas of 15.62 and 23.13 m² ha⁻¹, respectively, in deciduous and forest gallery forest types in a tropical dry forest reserve in Nicaragua. They also observed that in the deciduous forest small stems contributed to more than half of the basal area, whereas in the gallery forest large stems (>70 cm DBH) contributed to almost half the basal area.

A significant decrease in the basal area of 4.6 m² ha⁻¹ during the experimental period in treatment TFE was likely due to the effect of severe droughts in forest. Marín et al [16] also found a significant decrease in the basal area of 1.2% year⁻¹ in the deciduous forest and no change in the gallery forest when the stand dynamics and basal area change were analyzed in a tropical dry forest reserve in Nicaragua. Analysis of the intra-annual variability of data indicated that the basal area decreased from July to August because of the reduction in rainfall during the dry season. The values of biomass and basal area were similar to the findings of Baker et al [12] who found the biomass and basal area of 846 t ha⁻¹ and 38.9 m² ha⁻¹, respectively, for *terra firme* rainforest forest in the Amazon. Although episodic mortality occurs in the absence of climate change, the decrease in biomass of 17.1 t ha⁻¹ in the plot under normal climate during the period of record was considered

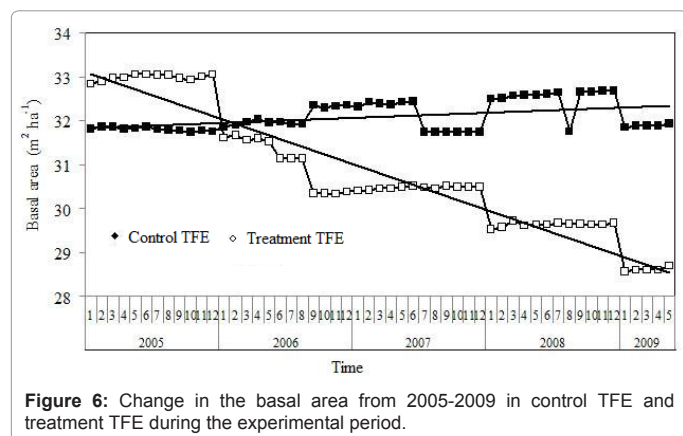


Figure 6: Change in the basal area from 2005-2009 in control TFE and treatment TFE during the experimental period.

abrupt. Analyzing a total of 2493 trees that died during the study period from 2001 to 2007 in Estonia, Laarmann et al [14] reported an average annual tree mortality rate of 1.3%, while grey alder (*Alnus incana* (L.) Moench) experienced the highest mortality rate (4.3%) but pine and spruce the lowest (0.9%). On the other hand, Stephens and Gill [17] found the cumulative tree mortality ranging from 2.7 to 3.6% and the annual rate of tree mortality of 0.162% year⁻¹ in north-western Mexico.

The extensive increase in tree mortality in both plots in 2005 was linked to anomalously warm sea surface temperatures in the North Atlantic which produced a hot and severe drought across the Amazon basin. The tree mortality rate in treatment TFE was high throughout the experimental period with the subsequent aboveground biomass loss, indicating the vulnerability of Amazonian rainforests to moisture stress. The percentage of trees that died from 2005 to 2009 in response to drought was 17% while in control TFE the percentage of trees that died was of 12%. Effectively, treatment TFE had a total of 86 trees that died through the period of record from 2005 to 2009, while control TFE had 62 dead trees. Therefore, more trees died in years that had below normal annual rainfall.

Another important finding is that dead trees were more frequent in the smallest class than in trees with DBH > 20 cm. Similar results were obtained by Guarín and Taylor [18] when analyzing the effects of drought for tree mortality in mixed conifer forests in Yosemite National Park, USA. Guarín and Taylor [18] also investigated the influence of drought on recent patterns of tree mortality in forests. They observed that the frequency of tree death dates was negatively correlated with annual and seasonal Palmer Drought Severity Index (PDSI) and the April snowpack depth, and more trees died in years with below normal PDSI and snowpack. Analyzing the sap flow data from a throughfall exclusion experiment in eastern Amazonian rain forest, Fisher et al [1] showed large dry season declines in transpiration, with tree water use restricted to 20% of that in the control plot at the peak of both dry seasons. These results suggest that the forest is not able to withstand a 50% reduction in rainfall over 1-2 years without impacting canopy gas exchange, and are in contrast with the results of Nepstad et al [19] for their TFE experiment, located in the Tapajo's national forest.

The frequency of tree death was associated with below normal moisture conditions over the experimental period. On the other hand, a higher coefficient of determination between tree mortality and biomass in treatment TFE indicated that mortality was higher for higher tree-size diversity during severe drought episodes. However, the relationship between biomass and mortality was less clear for treatment TFE with a low coefficient of determination, because the tree

mortality commonly involved multiple, interacting factors, ranging from particular sequences of climate stress and insect pests. Although the mortality rate was not significantly correlated with biomass in the plot under normal climate, the loss of aboveground biomass through mortality was decreasing for both plots. However, the mortality rate in control TFE was nonrandom with respect to tree size classes and species. Ganey and Vojta [20] found proportions of trees dying at the greatest rate in the largest size classes, particularly in mixed-conifer forest, where the mortality in the largest size class exceeded 22% from 2002 to 2007. These results indicate that the Amazonian rainforest is not resilient to severe droughts, and that treatments to increase the resilience of forest biodiversity to climate change may be appropriate. A drought can also reduce tree growth, increase tree mortality particularly on forest edges as well as increase leaf shedding. In this context, the Amazonian rainforest droughts have been strongly related to El Niño events [21]. However, declining rainfall over the Amazon region is likely to be impacting other anthropogenic forcing factors, such as deforestation and fires [22].

Conclusions

Experimental TFE, removing an estimated 50% of rainfall, caused soil drying and a resultant decrease in the basal area of 12.5% at the end of experimental period in May 2009 compared with the control plot. The tree mortality rate in treatment TFE was high throughout the experimental period with the subsequent aboveground biomass loss, indicating the vulnerability of Amazonian rainforests to moisture stress. The percentage of trees that died from 2005 to 2009 in response to drought was 17% while in control TFE the percentage of trees that died was of 12%. A significant environmental stress due to a long-term drought can have a profound impact on the vegetation dynamics in the Amazon region. The greater decrease in the aboveground biomass on treatment plots can be explained by reduced rainfall. The forest biomass is negatively correlated with tree mortality, especially on the rainfall exclusion plot, because mortality occurs in all size classes in both plots, with most mortality occurring in the subplot of higher tree-size diversity. The relationship between the aboveground biomass and mortality is less clear in normal climate with a low coefficient of determination. There was more mortality in 2005 than in 2006 to 2009 because of severe drought across the Amazon basin produced by the stronger El Niño in that year.

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