# EFFECTS OF FLOODING DURATION ON PLANT DEMOGRAPHY IN A BLACK-WATER FLOODPLAIN FOREST IN CENTRAL AMAZONIA

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**Abstract**
Rivers in central Amazonia experience annual water-level fluctuations of up to 14 m, flooding vast areas of forests for periods ranging from a few to 270 days per year. Several studies have demonstrated that differences in flooding duration affect species richness and plant distribution in Amazonian floodplain forests. There is an increase of species richness and diversity with decreasing flooding duration. However, the majority of the studies carried out in Amazonian floodplain forest were done with adult tree species, normally using trees with DBH ≥ 10 cm. The objective of this study was to test the hypothesis that there is an increase of species richness and that species composition changes along the flooding gradient if all plants with DBH ≥ 1 cm are included. To study the effects of flood duration on plant demography we surveyed the river margins of Rio Tarumã-Mirim, in the vicinity of Manaus, Brazil, which is seasonally flooded by black waters. The floodplains in the study area varied from 22 to 27 m AASL and all plants with DBH > 1 cm were inventoried in 144 plots of 10 x 10 m in size. A total of 159 tree species were found in all plots. The plants were divided into three DBH classes: (1) 1-4.9 cm, (2) 5-9.9 cm and (3) > 10 cm DBH. The analyses of these data showed that there is no difference of species richness in relation to topographic level in all DBH classes. However, species composition exhibited distinctive distribution patterns with respect to topographic levels in all DBH classes. We suggest that variation in species richness cannot be explained by a single environmental variable such as flooding duration. Factors such as soil type, slope, and distance to upland forests are also important in determining species richness in those forests. Differences in species distributions, independent of DBH classes probably are related to species ability to withstand seasonal flooding to different extents, and their differing tolerance and degree of adaptations which lead to a vegetation change along the hydrological or soil type gradient.
**Key words**: Amazonia, community ordination, floodplain forests, igapó, species richness, flood tolerance.

**Resumo**
Os rios na Amazônia central estão sujeitos a uma flutuação cíclica em seus níveis de até 14 metros, provocando a inundação de extensas áreas por períodos que variam de poucos dias a até 270 dias por ano. A maioria dos

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estudos nas áreas inundadas da Amazônia tem sido realizada normalmente com árvores adultas com DAP ≥ 10 cm. O objetivo deste estudo é testar a hipótese do aumento da riqueza e mudança na composição de espécies ao longo de um gradiente de inundação com plantas com DAP ≥ 1 cm. Este estudo foi realizado no rio Tarumã-Mirim, um afluente do rio Negro, sazonalmente inundado por água preta, próximo à cidade de Manaus, Amazonas, Brasil. O gradiente de inundação da área de estudo varia entre as cotas 22 a 27 metros em relação ao nível do mar. Neste gradiente de inundação foram colocadas 144 parcelas de 10 x 10 metros. Dentro de cada parcela todas as plantas com DAP ≥ 1 cm foram marcadas, medidas e identificadas ao nível mais específico possível. As plantas foram divididas em três classes de DAP: (1) 1-4.9 cm, (2) 5-9.9 cm e (3) > 10 cm. Foram identificadas 159 espécies arbóreas. Não houve diferença significativa na riqueza de espécies em relação ao gradiente de inundação e às classes de DAP. Contudo, há uma grande distinção na composição de espécies em relação ao gradiente de inundação em todas as classes de DAP. Nós sugerimos que a variação na riqueza de espécies pode ser explicada somente por uma variável ambiental, como a duração da inundação. Outros fatores, tais como, tipo de solo, declividade e a distância da floresta não alagada são também variáveis importantes na determinação da riqueza de espécies nas florestas inundadas da Amazônia. As diferenças na composição de espécies, independente da classe de DAP, estão relacionadas com a habilidade diferencial das espécies em tolerar os períodos de inundação ao longo do gradiente topográfico da área de estudo.
**Palavras chave:** Amazônia, ordenação de comunidades, florestas inundáveis, igapó, riqueza de espécies, tolerância a inundação.

## Introduction

In Brazilian floodplain forests, seasonal water levels can fluctuate by up to 14 m, and the flooding duration can vary from 50 to 270 days in the parts colonized by trees (Junk et al., 1989). The dramatic change from terrestrial to aquatic habitats during the year creates considerable stress for trees, and has resulted in adaptations for survival during long periods of total or partial submersion (Junk, 1989; Ferreira, 1997; Parolin, 2001; De Simone et al., 2002; Waldhoff et al., 2002; Parolin et al., 2004).

Local variation in topography in floodplain forests creates mosaics of different habitat types, which vary in terms of flooding duration, soil type, elevation, and distance from non-flooded forests (Junk, 1989). Although some studies have already been performed, which analyze plant distribution (Ferreira, 1997, 2000; Ferreira and Stohlgren, 1999), the nutrient-poor acidic blackwater forests (igapó) are still poorly understood. Contrary to nutrient-rich whitewater floodplains (várzea), where several studies which include the seedling and sapling stages have been performed (Wittmann and Junk, 2003; Conserva, 2006; Wittmann et al., 2006; Wittmann et al., 2010). In igapó all studies to date are based on the flood tolerance of adult individuals only.

Population studies of seedlings and saplings in different habitats and along flooding gradients in igapó floodplain forests are completely absent and it is necessary to complement our understanding of the mechanisms that determine richness, diversity and distribution of species in Amazonian floodplains.

The present study aims at quantifying the effect of flood duration on plant demography in an Amazonian igapó floodplain forest. The objective is to test the hypothesis that there is an increase of species richness and that species composition changes along the flooding gradient if all plants with DBH ≥ 1 cm are included. To study the effects of flood duration on plant demography we surveyed the river margins of Rio Tarumã-Mirim, in the vicinity of Manaus, Brazil, which is seasonally flooded by black waters.

## Methods

**Study area.** The study site was located on the lower course of the Rio Tarumã-Mirim, a tributary of the Rio Negro (3$^o$ 02' S; 60$^o$ 10' W), 20 km northeast of Manaus, seasonally inundated by black water rivers. Total annual precipitation in the region at an average is about 2300 mm. The amount of rain is typically irregularly distributed along the year, showing a marked dry season from June through September, and a rainy season from December to May. There is a time lag of several months between the peak of rainfall and maximum flooding. The study sites are between 22 and 27 m above sea level (ASL). The rising phase of Rio Tarumã-Mirim occurs between late December and early July, while the draining period occurs from late July to late November.

**Data collection.** The floodplain site was sampled in areas representing six different topographic levels varying from 22m to 27m ASL. 144 plots 10 x 10 m were randomly placed, varying from 15 to 25 plots in each topographic level. In each plot all plants > 1 cm diameter at breast height (DBH) were measured and identified in the field or collected for later identification in the herbarium. For demographic analyses, the plant community was divided into three classes in relation to DBH: 1) 1-4.9 cm DBH (saplings and young trees), 2) 5-9.9 cm DBH (young and adult trees) and 3) > 10 cm DBH (adult trees).

Measurements of water level were taken in each plot using the previous year's watermark on tree trunks, a reliable method which is commonly employed in this ecosystem. River level data were taken as equal to those measured in the same period at Manaus harbor since water-level differences between Rio Tarumã-mirim and the Rio Negro are negligible (Schmidt, 1976).

**Data analysis.** We used simple regression to test for differences in species richness in relation to topographic levels. We used a cluster analysis (McCune and Mefford, 1995) to determine differential distribution of species among the plots in the six topographic level, using the abundant species (>10 individuals overall) in the analyses.

## Results

**Species richness.** 159 tree species were identified in the plots sampled in this study, with 131, 126 and 102 species in the DBH classes 1, 2 and 3, respectively. There was an increasing accumulative number of new species in relation to the number of sampled plots, which was similar in the three DBH classes. No curve reached the asymptote (Figure 1). The increment of number of species is explained by the position of plots in relation to topographic level and results from species turnover along the flooding gradient.

There was no significant difference in species richness in relation to topographic level in the three DBH classes: (A) 1-4.9 cm; $r^2$= 0.02; $F_{[1,136]}$=3.36; p=0.069 (Figure 2), (B) 5-9.9 cm; $r^2$= 0.01; $F_{[1,138]}$=0.008; p=0.928 (Figure 3) and (C) > 10 cm; $r^2$= 0.001; $F_{[1,132]}$=0.072; p=0.789) (Figure 4).

**Species distribution.** There was a clear change in species distribution in relation to topographic level in the three DBH classes (Figure 5). In the cluster analysis, the plots situated in the low topographic levels 21 to 23 meters and subjected to longer periods of inundation were clearly separated from the other topographic levels (25-27 meters) in which they are subjected to intermediate and shortest periods of inundation (Figure 5).

The dominating species in the lowest level (21 to 23 meters) were *Symmeria paniculata*, *Licania apetala* and *Bactris bidentula, Quiina rhitidopus, Burdachia prismatocarpa* and *Eschweilera tenuifolia* (Table 1).

The dominating species in the higher levels (26 to 27 meters) were *Pentaclethra macroloba, Aspidosperma nitidum, Tovomita secunda, Trymatoccocus amazonicum* and *Mora paraensis* (Table 1).

## Discussion

The extreme differences in annual flood duration among the topographic level in the present study site (Ferreira and Stohlgren, 1999) do not necessarily lead to marked differences in species richness. This result is not consistent with the findings that flooding duration strongly affects species richness in Amazonian floodplain forests (Keel and Prance, 1979; Junk, 1989; Ayres, 1993; Ferreira, 1997; Wittmann et al., 2006).

There is some evidence that species richness in black water forest is affected by soil nutrients and not flooding duration (Prance, 1979). Black water forests on sandy soils, for example of the Rio Negro, sustain much poorer vegetation with lower species richness than those in black and white water forests on clayish soils (Takeuchi, 1962).

Ferreira (1997) reported a significant difference in species richness and diversity among plots situated in different elevations, in ephemeral lakes and river and stream margins in an igapó forest of Rio Jaú. Soil compositions between the habitats were quite distinct varying from sandy soils in the lake plots to clayish soils in the other sampled habitats. In the study carried out at Tarumã-Mirim river, the difference in species richness could be associated to a combination of flooding and soil composition. Furch (1997) determined that soil composition in the Tarumã-mirim site was homogeneous on all topographic levels.

We suggest that variation in species richness cannot be explained by a single environmental variable such as flooding duration. Factors such as soil type, slope, and distance to upland forests are also important in determining species richness in those forests. However, data availability is still limited due to the lack of replicates.

Although species richness may not be strongly influenced by the flooding gradient, our results support the hypothesis that differential tolerance to flooding results in a sequential change of species composition along the gradient, probably related to differences in physiological tolerances of species to flooding (Kozlowski, 1982; Junk, 1989; Parolin et al., 2004; Parolin, 2010; Parolin et al., 2010a). Kubitzki (1989) reported that metabolic adaptations might be decisive in controlling the floristic composition of floodplain forests. For example, dominant species in low topographic level region such as *Symmeria paniculata* and *Bactris bidentula* have anatomic and morphologic adaptations to support the long flooding duration that can extend to more 200 days by year (Parolin, 2010; Parolin et al., 2010b; Table 1).

Wittmann et al. (2004) related that species richness and distribution along the gradients of flooding and sedimentation are well defined in white-water floodplain forests in the Amazon. Only 2.6% of 222 recorded tree species occurred over the whole flood-level gradient.

Different sets of adaptations explain the strong gradient in species composition in relation to flooding duration (Takeuchi, 1962; Keel and Prance, 1979; Ferreira, 1997; Parolin et al., 2010b; Wittmann et al., 2010).

The cluster analysis showed clear plant assemblages in the different topographic levels in all DBH classes. As mentioned, plant distributions along the flooding gradient may be determined by differential tolerance of species to flooding duration which appears to be similar in all age classes of the plant species.

In conclusion, this study shows that in Rio Tarumã-Mirim variation in water level and flooding duration did not affect substantially plant species richness. However, a clear plant distribution along the flooding zones was evident, probably reflecting differences in flood tolerance among these species (Parolin et al., 2010b). While the latter pattern was expected, the former suggests that plant species richness in floodplain forests can be influenced by a more complex suite of factors than has previously been suggested.

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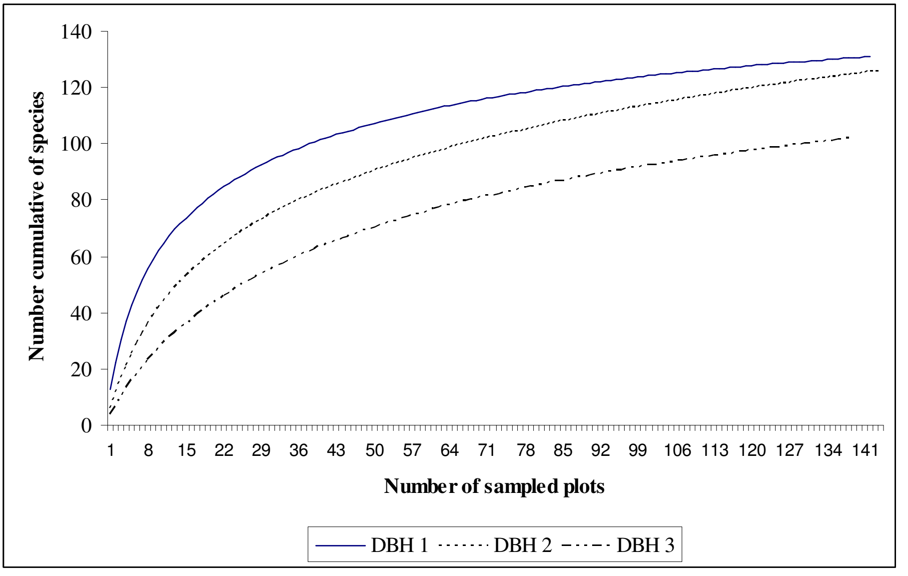


**Figure 1**:Cumulative number of species in relation to number of sampled plots by DBH class 1 (1-4.9 cm), class 2 (5-9.9 cm DBH) and class 3 (> 10 cm DBH) in the black-water floodplain forest sampled in this study.

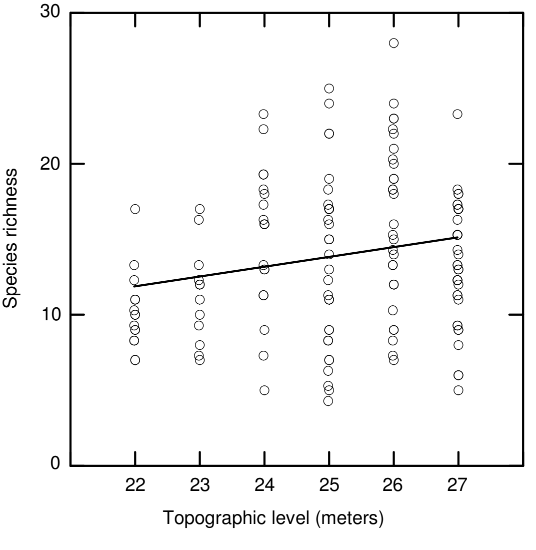


**Figure 2:**Relationships between species richness and topographic level in DBH class 1 (1-4.9 cm DBH) in the study area.

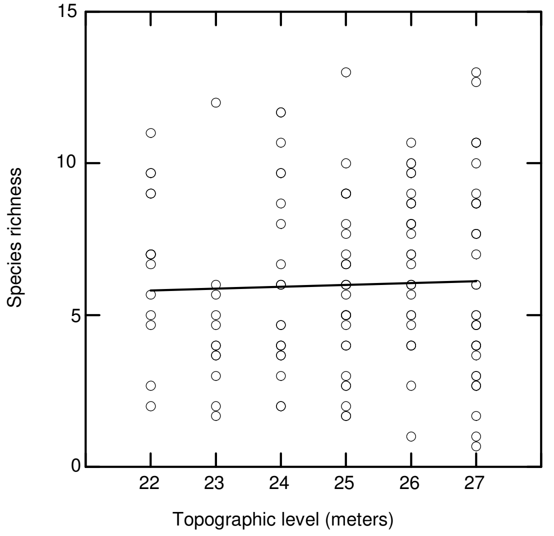


**Figure 3**:Relationships between species richness and topographic level in DBH class 2 (5-9.9 cm DBH) in the study area.

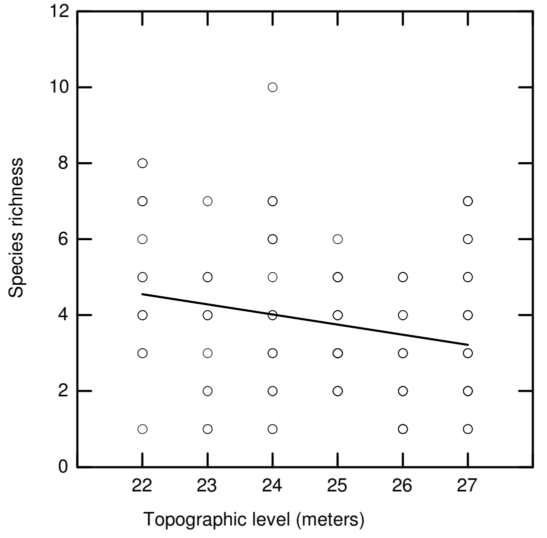


**Figure 4:**Relationships between species richness and topographic level in DBH class 3 (> 10 cm DBH) in the study area.

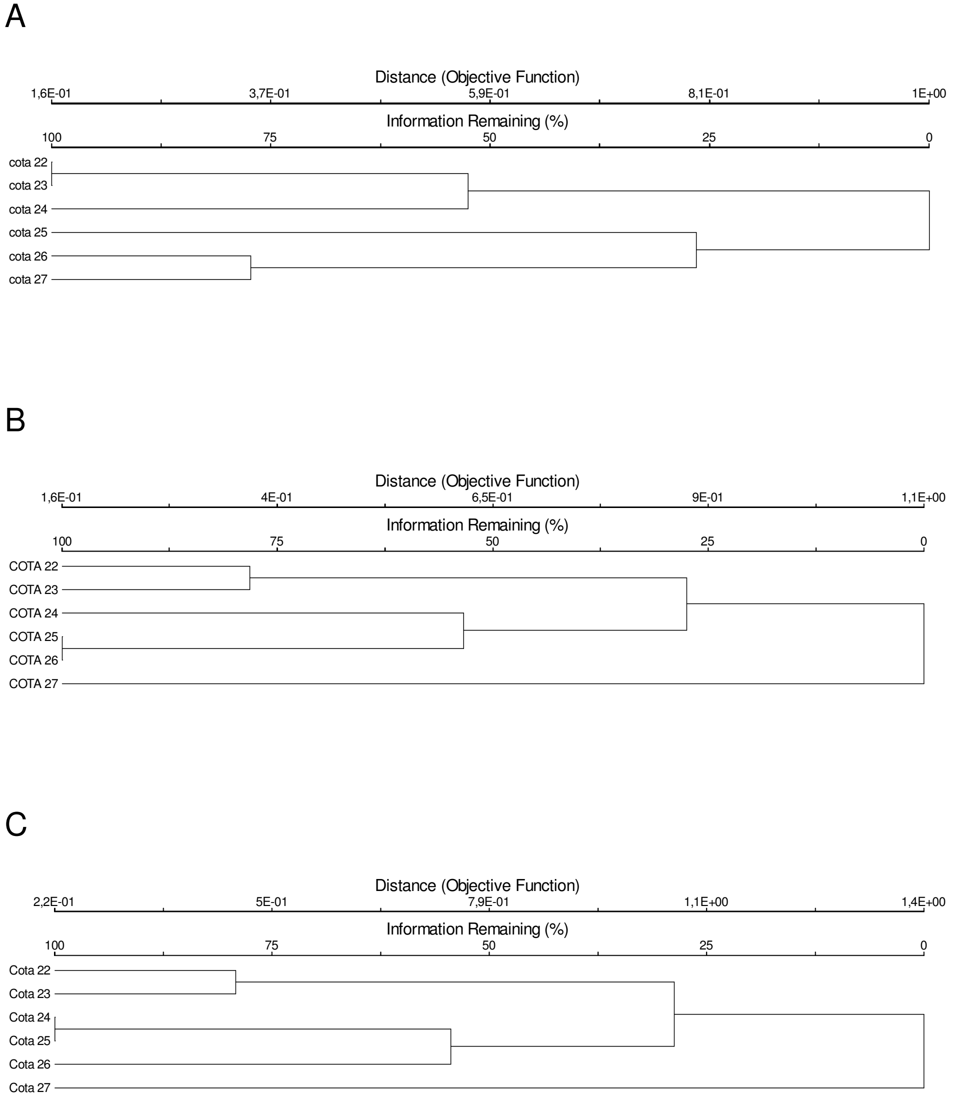


**Figure 5**:Cluster dendrogram of topographic level in relation to DBH Class 1 (1-4.9 cm) (A), Class 2 (5-9.9 cm) (B) and Class 3 (≥ 10 cm) (C), using the common species (highest 10 individuals)