Acta Oecologica 69 (2015) 21–30

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Effects of flooding on trees in the semi-deciduous transition forests of the Araguaia floodplain, Brazil

Dariusz Kurzatkowski, Christoph Leuschner, Jürgen Homeier*

Plant Ecology, Albrecht-von-Haller Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

A R T I C L E I N F O

Article history:
Received 24 February 2015
Received in revised form
18 August 2015
Accepted 18 August 2015
Available online 31 August 2015

Keywords:
AGB
Amazon
Drought
Flood level
Tree species diversity
Wood specific gravity

A B S T R A C T

The Araguaia floodplain, one of the large floodplain areas in the Neotropics, is located in the transition zone of Amazon forests and Cerrado. The region is characterized by annual floodings and a pronounced dry season of three months. We examined the influence of flooding from low to high terrain on floristic composition, forest structure and aboveground live biomass (AGB). We recorded all trees (dbh >5 cm) in 30 permanent plots (50 × 50 m) located at different topographic positions across a flooding gradient.

Sixty-nine tree species from 30 plant families were recorded; Fabaceae (15 species) was the most abundant family, followed by Myrtaceae (5), Anacardiaceae (4) and Rubiaceae (4). Family composition was similar to Central Amazonian floodplain forests and many widely distributed flood-tolerant tree species were shared. Tree species richness was relatively low with 14–31 tree species per plot and was not affected by flood level, but tree species composition and family importance values differed markedly between annually flooded and non-annually flooded forest stands.

Forest top canopy height varied between 10.5 and 18.5 m and was negatively correlated with flood level ($R^2 = 0.25$, $p = 0.002$). Mean wood specific gravity (WSG) of the plots increased with the flood level ($R^2 = 0.43$, $p < 0.001$) and apparently was unrelated to drought intensity. Stem density (plot mean 1040 ha^{-1}), mean dbh, tree basal area (19.4 m^2 ha^{-1}) and AGB (116.8 Mg ha^{-1}) were not dependent on flood level. The low AGB compared to Central Amazonian floodplain forests is probably a result of the pronounced dry season and limited nutrient availability in the igapó forests of the Araguaia floodplain. In view of the predicted increase of extended drought periods with global warming, we assume that future forests in the study area may lose some or all drought-sensitive tree species and likely may face a reduction in AGB.

1. Introduction

Tropical floodplain forests are unique ecosystems which harbor a wealth of plant and animal species with specific adaptations to seasonal flooding and anoxia (Junk, 1989). Freshwater floodplains cover an area of approximately 1.7 million square kilometers within the Amazon basin and include seasonally inundated forests, riparian zones, swamps, and bogs (Junk et al., 2011). With an extension of approximately 550,000 km^2, large-river floodplains fringing the Amazon River and its major tributaries account for approximately 7–8% of the Amazon basin (Melack and Hess, 2010, Junk et al., 2011). Most research on these systems has been conducted in the Central Amazonian várzea and igapó forests in a tropical humid climate. However, floodplain forests are also present at the margins of the humid tropical realm in the transition zone to tropical semi-arid climates.

Seasonal flooding contributes significantly to biodiversity (Gopal et al., 2000) and affects plant communities in many aspects. The structure, floristic composition and tree species richness of inundation forests are tightly linked to their position in the flood-level gradient (Junk, 1989; Ayres, 1993), but also depend on sediment characteristics determined by the dynamic geomorphology of the river system. Seasonal inundation and associated anoxia often result in reduced metabolic activity, inhibition of photosynthesis and growth depressions of the trees (Worbes, 1985; Joly, 1994; Parolin, 2001; Herrera, 2013). In certain species, inundation triggers the formation of hypertrophic lenticels on the stem bark, of extended aerenchyma in the roots and other anatomical and morphologic adaptations to oxygen deficiency (Kozlowski, 1984; Junk, 1996; Piedade et al., 2000; Parolin et al., 2002).

* Corresponding author.
E-mail address: jhomeie@gwdg.de (J. Homeier).

http://dx.doi.org/10.1016/j.actao.2015.08.002
1146-609X/

Some of the tree species of the várzea and igapó forests are widespread particularly in semi-deciduous forests and savannas of the Neotropis (Prance, 1979). Junk (1989) and Worbes (1997) assume that those widespread species do not possess primary adaptations to flooding, but generally are tolerant to seasonal impairment of growing conditions. Ter Steege et al. (2003) and Wittmann et al. (2006a) observed that the inundated Amazon forest is characterized by a trend of decreasing tree species diversity from the West to the East. Apart from this gradient, tree diversity generally decreases with the length of the flooding period due to the selective pressure imposed on the trees to adapt to this extreme habitat (Junk, 1989; Ferreira, 1991; Wittmann et al., 2006a). In savanna areas, plants have to deal with alternating periods of flooding and water limitation (Parolin et al., 2010), and the severe drought stress that often characterizes the terrestrial phase favors a mixture of savanna vegetation and forested patches (Lourival et al., 2011; Nunes da Cunha and Junk, 2011).

The Araguaia floodplain forest is the fifth largest floodplain area in South America with a total area of 59.000 km^2. It is located at the south-eastern fringe of the Amazon forest in the transition zone between tropical moist and tropical dry forest (cerrado) with a pronounced dry period of four to five months. Araguaia River is a clear water river and the floodplain vegetation could be classified as clear water igapó (Junk et al., 2011). The majority of central Amazonian wetlands are forested (Schöngart et al., 2010; Wittmann et al., 2010; Wittmann, 2013). While the immediate study region is covered by large tracts of natural forest vegetation well-preserved in Cantão State Park, the greater Araguaia floodplain is part of the so-called 'Arc of deforestation' in southern Amazonia which is under heavy pressure by human expansion.

The floodplain forests are usually exposed to several months of flooding followed by a period with marked soil desiccation. Combined measurements of evapotranspiration and soil hydrology in the study area have shown that the groundwater table is closely linked to the river water level and that the vegetation is sensitive to extended drought periods (Borma et al., 2009). So it can be assumed that more elevated stands should be stronger affected by drought during the dry season.

In the semi-arid floodplain forests of the Araguaia floodplain and elsewhere, trees have to cope with long periods of flooding and with seasonal drought as well. Thus, tree growth is hampered by two main stressors in the course of a year, but as reported by Parolin (2010) and Parolin et al. (2010), many of the adaptations to survive flooding (e.g., sclerophyllous leaves) are also beneficial under drought stress. We expect that the standing biomass of these drought-affected floodplain forests is smaller than in the várzea and igapó forests of the humid Amazon. However, this type of floodplain forest has so far received much less attention than the impressive floodplain forest ecosystems of central Amazonia. This is unsatisfactory because knowing the carbon stores and C sequestration of this type of floodplain forest at the margin of the Amazon would improve our understanding of the carbon balance of the Amazon basin (Schimel 1995; Houghton et al. 2000; Ketterings et al. 2001). Further, the biodiversity and ecology of these unique ecosystems in the transition zone of tropical moist to dry forest is only poorly understood.

This study examines the variability of floristic composition and forest structure and estimates the aboveground coarse woody biomass (AGB) in 30 plots located at different topographic positions in a tropical floodplain forest (Araguaia system) at the south-eastern fringe of the Amazon which is exposed to a marked dry season. We predicted that tree species composition changes with increasing maximum height of inundation level from a community composed of drought-adapted, flooding-sensitive tree species at highest terrain to a flooding-tolerant, drought-sensitive assemblage close to the river. Due to the existence of two opposing stress gradients from low to high terrain, we further assumed that AGB in this forest is generally lower than in the moist floodplain forests of the Central Amazon. We expected AGB to show a hump-shaped distribution along the elevation gradient with biomass peaking at sites with only low to moderate water levels during inundation where stress due to both anoxia and drought is probably lowest.

Since tree species richness is negatively affected by height and duration of flooding in Amazonian inundation forests (e.g., Wittmann et al., 2006a), we further predicted that α-diversity declines from higher to lower terrain with increasing maximum flood level height. Our study also delivers basic information on the structure and species composition of a poorly studied tropical forest type that is under pressure not only through deforestation but also by recent climate warming with extended drought periods at the margins of the Amazon basin (e.g. Olivares et al., 2015).

2. Materials and methods

2.1. Study area

The study area is located in the southern part of Cantão State Park in Tocantins State in the south-eastern Brazilian Amazon (Fig. 1). The study region is part of the transition area between the Amazon forest in the west and cerrado vegetation in the east (Brazilian Institute of Geography and Statistic, IBGE). Cantão State Park belongs to the Araguaia river floodplain (Eiten, 1985) and is covered by large areas of intact moist forest and patches of cerrado on drier soil.

The soils of the study sites are quite variable ranging from upland red–yellow and yellow Oxisols and red–yellow Ultisols to alluvial soils with hydromorphic lateritic and gleyic characteristics (DNPM, 1978). The soils on the floodplain are acid and nutrient-poor Dystrophic Plinthosols and Gleysols (Martins and Kardec, 2006).

The climate of the region is hot and semi-humid (Fig. 2) with an average annual precipitation of 1755 mm. The rainy period lasts from November to April, followed by a distinct dry season from June to September with monthly precipitation of 50 mm or less. The average annual temperature is 26 °C, the highest mean monthly temperature is 30 °C in August and September, while the lowest mean monthly temperature is 22 °C in July. Relative air humidity varies between 80% in the rainy and 60% in the dry season.

2.2. Study plots

The study plots are located on the right bank of Javaés River within an area of 10 km^2; the distance to the Canguçu Research Center (CRC; 9°58′41″S, 50°02′12″W) is 0.2–5 km. We established 30 plots with a size of 50 × 50 m (0.25 ha) in order to study changes in forest vegetation in relation to variation in flood level height. For plot selection, we avoided canopy gaps and early successional stages. The distance of the plots to Javaés River varied between 0.1 and 1.5 km. The 30 study plots cover a total forest area of 7.5 ha. The maximum flood level in a plot was defined as the distance from the soil surface to the upper limit of the dark water mark visible on the trees trunks. Measurements were done in eight subsequent years (2001–2008) at the start of the dry season in the four corners of each plot.

Study plots were divided into the following two groups to compare effects of flooding during our observation period: 1) non-annually flooded (NAF) stands, where the flooding occurred not regularly and maximum flood level over ground was 1.0 m with inundation periods of up to two months and 2) annually flooded