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Litter and nutrient flows in tropical upland forest flooded by a hydropower plant in the Amazonian basin

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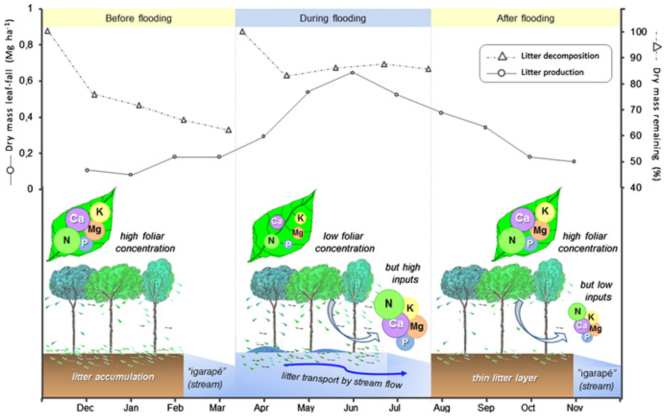
HIGHLIGHTS

- Flooding by dams increases litter production in upland forests during dry seasons.
- Flooding retards litter decomposition, but does not favor litter accumulation.
- Upland forests double nutrient inputs when flooded, but reduce leaf concentration.
- This is a forest strategy to prevent biomass nutrient depletion during flooding.
- These alterations may have consequences for regional and global carbon balance.

GRAPHICAL ABSTRACT



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ABSTRACT

Extensive areas in the Brazilian Amazon have been flooded for the construction of hydroelectric dams. However, the water regime of these areas affects the dynamics of *igarapés* (streams) in adjacent *terra firme* (upland forests). When the reservoirs are filled, the water levels of streams rise above the normal levels and upland bank forests are flooded. We investigated how this flooding affects the litterfall and nutrient input in the upland forests upstream of a hydroelectric dam reservoir in the Central Amazonia. When the reservoir was filled, the forests were flooded and produced more than twice the litter (8.80 $\text{Mg}\cdot\text{ha}^{-1}\ \text{yr}^{-1}$), with three times more leaves (6.36 $\text{Mg}\cdot\text{ha}^{-1}\ \text{yr}^{-1}$) than when they were not flooded (4.20 and 1.92 $\text{Mg}\cdot\text{ha}^{-1}\ \text{yr}^{-1}$, respectively). During flooding, the decomposition rate was four times lower in flooded forests (0.328 $\text{g}\cdot\text{g}^{-1}\ \text{yr}^{-1}$) than in control forests (1.460 $\text{g}\cdot\text{g}^{-1}\ \text{yr}^{-1}$). Despite this, the flooding did not favor litter or nutrient accumulation. Therefore, dam construction changes the organic matter and nutrient cycling in upland Amazon rainforests. This may influence the important role that they play in organic matter dynamics and could have consequences for the regional carbon balance and, ultimately, global climate.

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1. Introduction

A section of the Amazon forest that extends over *várzea* lowlands (floodplain forests) along the main rivers is flooded in the rainy seasons (Prance, 1979). However, most of the basin is composed of *terra firme* (upland forests) which are not subject to this natural flooding caused by large rivers (Haugaasen and Peres, 2006). This upland forest cover has been reduced due to land use changes in the Amazon region, including the construction of hydroelectric plants (Fearnside, 2005; 2016a). For the implementation of hydroelectric plants, dams are constructed in large rivers to form reservoirs and provide power generation. Thus, extensive upland forests are replaced by permanently flooded areas within reservoirs, and there is then periodic flooding of adjacent upland forests (Gonçalves et al., 2012).

When upland forests are flooded, the trees do not adapt to the new conditions, and they adjust their metabolism in an attempt to survive (Santos Junior et al., 2013). Initially, the trees reduce their rates of respiration and photosynthesis (Ferreira et al., 2007), which lowers the capacity of the forest to fix carbon as biomass (Santos Junior et al., 2015; Ferreira et al., 2009). In addition to reducing carbon fixation, flooding triggers physiological mechanisms that stimulate early senescence of plant material in tree canopies (He et al., 1996). Therefore, the flooding of upland forests is expected to increase leaf litter production by trees, which has the potential to increase the concentrations of nutrients in the soil.

In addition to these effects on vegetation during flooding, water fills the pores of the soil, and the remaining oxygen is rapidly consumed by aerobic organisms (Dat et al., 2004; Souza et al., 2009). As a result, there is low oxygen availability in the soil surface a few days after the onset of flooding and oxygen may become unavailable in lower layers (Camargo et al., 1999; Unger et al., 2009). This causes organic matter to be decomposed by anaerobic organisms, which are relatively slow decomposers (Dat et al., 2004). Thus, flooding is expected to slow the rate of litter decomposition and mineralization of nutrients, favoring the accumulation of litter and nutrients on forest soil. The construction of dams in the Amazon basin is thus expected to modify the biogeochemical cycling of organic matter and nutrients in upland forests.

The Brazilian Amazon has 15 “large” dams (defined in Brazil as >30 MW installed capacity) in operation on its main rivers (Fearnside, 2016a). The construction of 37 additional large dams in the Amazon is planned as part of the infrastructure planning of the Brazilian federal government (Fearnside, 2016a). Eighteen of the planned dams would have a total installed capacity up to 2021 (Brazil, 2014). Including small hydropower plants (<1 MW), the planned number of hydroelectric dams in the Amazon is 334 (Zarfl et al., 2015). Together, these plants will flood >100,000 km^2 of upland forests (Fearnside, 2005) and will produce periodic flooding events in adjacent forests (Gonçalves et al., 2012). Given this expansion of the network of hydroelectric power stations in the Amazon basin, the present study aimed to investigate how this flooding affects litter and nutrient cycling in upland Amazon rainforests. The following hypotheses were tested: (i) flooding increases litter fall in upland forests and, therefore, (ii) increases nutrient inputs to soil; (iii) flooding slow litter decomposition and the release of nutrients from this layer; thus, (iv) litter and nutrients accumulate in upland forest soils when they are flooded.

2. Materials and methods

2.1. Study areas

The study was conducted in upland forests of the Central Amazon adjacent to the Balbina hydroelectric reservoir (0°50′ to 1°55′ S, 58° 50′ to 60°10′ W). The plant is located approximately 140 km north of Manaus (Amazonas State, Brazil). The forests are located in the basin of the *Uatumã* River, a tributary of the *Amazonas* River. The topography of the region consists of rugged mountains, with lowland areas, slopes and an upland plateau (Costa et al., 2008). Strongly acidic and nutrient-poor Ultisols and Oxisols are the predominant soils (Quesada et al., 2011) and have been identified as red-yellow ultisols and red-yellow oxisols (IBAMA, 1997). There is generally low phosphorus (P) availability, but P surface availability increases in the soil after flooding events, whereas the soil concentration of nitrogen (N) is lower (Pereira, 2013).

The climate of the region is of the “Amw” type, i.e. a hot and humid tropical climate, according to the Köppen classification (Peel et al., 2007), with an average monthly temperature of 27 °C and average annual rainfall of 2200 mm (Greenberg, 2012). February and March are the wettest months (306 and 371 mm of precipitation per month, respectively), and June, July and August are the driest months (75, 126, and 25 mm of precipitation per month, respectively), as well as the hottest months (25.9, 25.8, and 27.5 °C, respectively) in the *Uatumã* River Basin (INMET, 2013; LBA-DIS, 2013).

The upland vegetation is classified as dense rainforest and reaches a height of up to 40 m with emergent trees up to 50 m (Costa et al., 2008). There is a predominance of tall, slender trees with a diameter at breast height (DBH) from 0.10 to 0.30 m, but there are individuals with a DBH ≥ 0.80 m. In the middle stratum, the height of individual trees ranges between 3 and 9 m, and 0.15 m DBH predominates. The forest understory is dense, with individuals up to 0.5 m in height (Amaral et al., 2000).

The reservoir of the Balbina hydroelectric plant was formed in the *Uatumã* River in 1987 (Fearnside, 1990). The construction of the dam flooded nearly 3000 km^2 of upland forest (Costa et al., 2008). Some continuous upland forests upstream of the dam, adjacent to the reservoirs, were not permanently flooded. Nevertheless, they were affected by the reservoir, because the periods of high and low water in the reservoir are opposite the seasonality of rains. In the dry season, the dam gates are closed, and the water level rises inside the reservoir. As the water level in the reservoir rises, the water level in *igarapés* (streams) rises above the normal level and overflows into the upland forest growing on its banks. This artificial flooding occurs during the dry season and upland forests remain flooded for two to four months (late March through August). In the rainy season, the dam gates are opened, and the reservoir water level recedes. As the water levels in the reservoir decrease, the *igarapés* (streams) water levels are also significantly lowered; subsequently, aquatic macrophytes die, and grasses grow on the forest soil. This low-water period occurs during the rainy season (late September to early March). After flooding these soils dry and the forests return to a natural upland condition. Thus, changes in reservoir water levels periodically flood upland forest areas growing on its banks for two to four months a year.

2.2. Sampling design

To test how this artificial flooding affects nutrient cycling in upland rainforests, sampling units were randomized in continuous upland forests located on the right and left banks of two *igarapés* (streams) adjacent to the reservoir. For allocation of the sampling units, seventeen randomized measures were obtained, by lot, along the entire length of the streams (3.5 km). After randomization and allocation of the units, GPS data (WGS84) indicated that the minimum distance between two sampling units was 0.13 km. Due to the low average wind speed registered in this region during the study (11.1 km h^{-1}; LBA-DIS, 2013), it is very unlikely that litter would be transported between the units by wind (Andrade et al., 1999; Scoriza et al., 2012). Therefore, the minimum distance between sampling units ensured the independence of 17 sampling units for the hypotheses under evaluation.

Each sampling unit consisted of two paired upland forests: one upland forest near the stream that was artificially flooded—“*flooded forest*”—and an undisturbed upland forest that was never artificially flooded—“*control forest*”—located 20 m from the flooded forest. The distance of 20 m between the paired forests within each sampling unit was sufficient to sample the different environmental conditions (flooded