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Above-ground woody biomass distribution in Amazonian floodplain forests: Effects of hydroperiod and substrate properties

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ABSTRACT

The importance of tropical forests in regulating global carbon stocks is well known. However, the role of abiotic variables related to climate conditions and edaphic parameters for patterns of above-ground woody biomass (AGWB) are still under debate. For Amazonian forests subjected to periodic floods, these patterns are even more uncertain. This study aimed to evaluate AGWB stocks in Amazonian floodplain forest, and investigate the importance of forest structure, hydroperiod and edaphic parameters for AGWB. Results are based on floristic inventories conducted in twelve hectares of forest distributed across four floodplains. All trees ≥ 10 cm DBH were tagged, identified, and had their DBH and height measured. Allometric equations were applied for calculating AGWB. Hydroperiod was estimated for each sample plot, and soil samples were collected and chemical and physical components analyzed. Hierarchical partitioning was applied to determine importance of forest structure variables for AGWB, and GLMMs to evaluate the individual role of several edaphic parameters and hydroperiod for AGWB stocks. AGWB estimates varied substantially both between and within sites, as did the proportional contribution of forest structure variables to AGWB. Fabaceae contributed most to AGWB overall, and hydroperiod was more important than soil fertility in explaining variation in AGWB values. Amongst the edaphic variables, Iron (Fe) was the component that influenced AGWB the most, followed by Aluminium (Al) and Phosphorus (P). Overall, our results indicate that, on the investigated Amazonian floodplains, AGWB is mainly driven by hydroperiod rather than edaphic properties. This occurs despite a constant input of nutrients caused by flooding events. In addition, this is the first study to suggest that P appears to be of some importance in Amazonian várzea and paleo-várzea floodplains, where soil fertility is generally higher than in non-flooded terra firme forests.

1. Introduction

Reducing Emissions from Deforestation and Degradation (REDD) is a United Nations Framework Convention on Climate Change (UNFCCC) program to offer financial incentives to developing countries to curb forest carbon emissions. This scheme, which has been amplified in scope and ambition as REDD+, can also indirectly support biodiversity conservation through reduced habitat loss and degradation. These efforts currently focus on tropical forest countries for several reasons. Tropical forests cover only ~7% of the global land area, but store as much as 55% of all terrestrial carbon in its vegetation (Pan et al., 2011). Additionally, tropical forests annually process around six times more carbon via photosynthesis and respiration than that in all fossil fuel emissions (Malhi and Grace, 2000; Lewis et al., 2009). Deforestation rates are also higher in tropical forests than elsewhere (Achard et al., 2002; Santilli et al., 2005). This forest clearing and degradation account for roughly 15% of current global greenhouse gas emissions, making it the second most important contributor to climate change after fossil fuel combustion (Houghton, 2005).

Tropical forests also play a pivotal role in mitigating climate change by absorbing nearly one-fifth of the annual CO_2 released by fossil fuels around the globe (Lewis et al., 2009) and recycling nearly half of all precipitation as evapotranspiration (Avissar and Werth, 2005). In fact, there is mounting evidence that undisturbed old-growth tropical forests

Abbreviations: AGWB, above-ground woody biomass; GLMM, generalized linear mixed models

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may be accelerating in growth (Lewis et al., 2004) and increasing in biomass and carbon (Malhi and Grace, 2000; Baker et al., 2004a), possibly in response to a CO_2 fertilization effect; i.e. elevated atmospheric CO_2 concentrations (Malhi and Grace, 2000). Yet alternative hypotheses suggest that any evidence of biomass accumulation is simply a local response to forest recovery from natural and human disturbances. For example, severe El Niño events cause elevated tree mortality (Condit et al., 1995; Laurance et al., 2001) and recent estimates indicate that natural tropical forest regeneration currently removes 1.6 Pg C yr^{-1} from the atmosphere (Pan et al., 2011).

Yet, despite their obvious importance for the global carbon budget, the total amount of carbon stored in tropical forests is still under intense debate. This is underlined by global values ranging from 158 to 324 Pg C (Gibbs et al., 2007; Baraloto et al., 2011). There is therefore an urgent need to improve our understanding of how different factors affect the spatial and temporal variation in above-ground woody biomass (AGWB) in the tropics (Gullison et al., 2007; Baraloto et al., 2011).

Several studies have reported a role for climatic variables in determining patterns of AGWB within tropical forests. For instance, regional variation of AGWB was positively related to annual precipitation across Amazonia, while dry season length had a negative impact on AGWB (Chave et al., 2004; Malhi et al., 2006). However, other studies found no effect of water availability and claim that AGWB in the Amazon is mainly influenced by forest structure variables, such as basal area (Baker et al., 2004b; Malhi et al., 2006; Paoli et al., 2008), number of large trees (DeWalt and Chave, 2004; Paoli et al., 2008; Rutishauser et al., 2010), mean tree height (Chave et al., 2005), mean wood specific gravity (Baker et al., 2004b; DeWalt and Chave, 2004; Stegen et al., 2009) and, maximum individual biomass (Stegen et al., 2011).

Soil properties, including drainage ability, have also been repeatedly reported as highly important for variation in species composition and other forest structure components at large (e.g. ter Steege et al., 1993; Ruokolainen et al., 1997; Sollins, 1998) and local scales (Clark et al.,1995; Condit et al., 2013). For example, changes in AGWB have been attributed to soil fertility (DeWalt and Chave, 2004; Paoli et al., 2008; Quesada et al., 2009). However, most studies have been conducted at large spatial scales and few studies have analyzed the effects of soil fertility on AGWB at local scales (Laurance et al., 1999; Ferry et al., 2010). Moreover, a common denominator for existing studies is that the vast majority have been conducted in upland terra firme forest (i.e. forests not subjected to periodic flooding). A more refined understanding of how different environmental variables affect patterns of AGWB across different forest types in Amazonia is therefore lacking.

In Amazonia, floodplain forests subjected to predictable, long-lasting, and monomodal flood pulses cover vast areas (Melack and Hess, 2010; Junk et al., 2011). These floodplains are divided into different types based on the hydro-chemical properties of the rivers that inundate them. The two major floodplain systems in Amazonia are called várzea and igapó. Várzea forests occupy approximately 450,000 km^2 and occur along white-water rivers rich in Tertiary/Quaternary sediments originating from the Andes or pre-Andean regions. Due to the annual deposition of nutrient rich sediments, these forests are highly fertile (Junk et al., 2011). Igapó forests cover an area of approximately 300,000 km^2 and occur on floodplains along black- and clear-water rivers that carry small amounts of Tertiary sediment originating from the Guyana and Central Brazilian Shields (Sioli, 1965; Prance, 1979; Melack and Hess, 2010; Junk et al., 2011). These are low fertility systems, as they lack the significant seasonal input of nutrient rich sediments (Junk et al., 2011). A third, but less extensive, floodplain type was also recently supported based on an analysis of tree species composition - paleo-várzea (Assis et al., 2015a). It covers approximately 125,000 km^2 and occurs on fluvial Andean deposits that have been abandoned by white-water rivers. These floodplains are inundated by small to intermediate black-water rivers that originate in cratonic areas and carry these already once-deposited paleo-sediments (Junk et al., 2011).

Amazonian floodplains are subjected to floods that may last for several months during the course of the year. The effects of waterlogging include oxygen deficiency at the root level, and a reduction in photosynthesis and tree growth during inundation (Parolin et al., 2004; Parolin, 2009; Schöngart et al., 2002). To cope with the annual flood pulse, tree species that inhabit the Amazonian floodplains have therefore developed a range of phenological, physiological, and structural adaptations. These strategies may strongly influence the AGWB in these ecosystems (Hawes et al., 2012). For example, tree species portray rapid growth rates in várzea forests due to the fertile alluvial soils. This, and the highly dynamic nature of white-water rivers, favour the presence of species with relatively low wood specific gravity (Worbes et al., 1992; Baker et al., 2004b; Wittmann et al., 2006). In addition, disturbance caused by inundation and related geomorphic dynamics appears to restrict tree height, explaining why Amazonian floodplain trees are generally lower than their terra firme counterparts (Souza and Martins, 2005). Such variation between different forest types across Amazonia underline the importance of habitat-specific AGWB estimates to more adequately account for the role of Amazonian forests in the global carbon budget.

Yet, there are few studies investigating potential changes in AGWB along environmental gradients in the Amazon, particularly within floodplains. One exception is that of Hawes et al. (2012), who observed that várzea forest biomass was higher in plots subjected to longer flood duration. However, the effects of flooding on forest parameters (including AGWB) are known to be intimately associated with edaphic variables (Wittmann et al., 2010; Assis et al., 2015b, Targhetta et al., 2015). It is therefore only possible to disentangle the influence of edaphic variables and flooding on AGWB by jointly considering these gradients. The main objective of this study was to estimate AGWB across four different floodplain forests in central-western Amazonia and evaluate how AGWB is related to hydroperiod and soil properties. More specifically, we addressed the following questions: (i) how do forest structure and species composition on the different floodplains affect AGWB patterns? and (ii) what is the role of edaphic variables and the hydroperiod in determining patterns of AGWB?

2. Material and methods

2.1. Study areas

Floristic inventories were conducted in four floodplain forests along different tributaries of the Solimões (=Amazon) river: Purus (S4°19′; W61°52′), Tefé (S4°9′; W65°6′), Juruá (S3°14′; W66°3′) and Jutaí (S3°22′; W67°28′; Fig. 1). All study areas are located at approximately the same latitude (2° S), but are separated longitudinally by a minimum and maximum distance of 120 and 600 km, respectively. The floodplain forests at each site are affected by an annual, long-lasting (> 5 months) flood pulse, so the trees are subjected to alternating terrestrial and aquatic phases with a seasonal inundation of up to 230 days per year (flood pulse, *sensu* Junk et al., 1989). The forests surveyed are considered pristine as they are located distant of urban centres. Annual rainfall averages approximately 2800, 2700, 2500 and 2600 mm, for Jutaí, Juruá, Tefé and Purus, respectively. None of these areas have more than one month per year with rainfall < 100 mm (Sombroek, 2001).

The Purus and Juruá rivers are white-water rivers carrying large amounts of nutrient-rich sediments from the Andes. Floodplains along these rivers are thus classified as várzea and their substrates are highly fertile. The Tefé and Jutaí rivers carry paleo-sediments originating from the Andes, and are therefore classed as floodplain paleo-várzeas (Junk et al., 2011; Assis et al., 2015a).

2.2. Floristic inventories

Floristic inventories were conducted during the 2009 and 2010 low-