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Aboveground net primary productivity in tropical forest regrowth increases following wetter dry-seasons

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ABSTRACT

Aboveground net primary productivity (ANPP) represents an important integrated measure of resource effects on forest ecosystem functions. Rates of ANPP, as well as resource availability controls over ANPP, are poorly understood for tropical forest regrowth following agricultural abandonment, although such regrowth accounts for a large and growing proportion of tropical landscapes. Here, we report on the response of ANPP to inter-annual variability in dry-season precipitation and to four years of dry-season irrigation in a forest regrowth stand in eastern Amazonia. ANPP was most strongly correlated with previous-year annual and dry-season precipitation inputs, suggesting a lag effect of the influence of precipitation on ANPP. The dry-season irrigation experiment provides some confirmation of this lag effect: ANPP response to treatment was significant for 2002 and 2003, following strong previous-year dry seasons, but not during the first treatment year (2001) or 2004, following the weak 2003 dry season. ANPP response to both inter-annual precipitation variability and to dry-season was largely due to a response in aboveground biomass increment rather than litterfall. Drought constraints on aboveground biomass increment suggest that the potential of forest regrowth to sequester atmospheric carbon will decrease with projected reductions in regional rainfall.

1. Introduction

Net primary productivity (NPP) is considered to be the best integrator measure of resource effects on ecosystem processes (Chapin and Eviner, 2003). Improved understanding of temporal shifts in NPP may aid predictions of ecosystem response to ongoing climate and land-use changes (Tian et al., 1998). In tropical forests, reliable estimates of NPP generally refer to aboveground net primary productivity components (ANPP) because belowground NPP is notoriously difficult to measure (Clark et al., 2001b). For tropical forest regrowth (e.g. following agricultural conversion and abandonment), there are few reliable estimates of ANPP, because the successional studies common to the research of tropical forest regrowth typically rely on chronosequences rather than on longitudinal analyses (Zarin et al., 2001).

Aboveground biomass increment in live trees (i.e., mostly wood increment) and non-woody litterfall (a proxy for leaf production) may be summed to estimate ANPP; both aboveground biomass increment and non-woody litterfall can be relatively easily measured and represent two significant components of total ANPP (Clark et al., 2001a). Stem diameter and height measures are usually used to estimate aboveground biomass (AGB) through allometric equations (e.g., Ducey et al., 2009). Despite several reports on AGB for tropical forest regrowth (Saldarriaga et al., 1988; Zarin et al., 2001; Gehring et al., 2005), repeated measures of AGB and litterfall are rare and calculations of ANPP for these forests are therefore lacking.

Observational and manipulative experiments suggest that moisture availability may be an important control over ANPP in tropical forests. At old-growth forest sites in the Brazilian Amazon, higher diameter growth rates are associated with wetter periods (Higuchi et al., 2003; Rice et al., 2004; Vieira et al., 2004). Brando et al. (2008) and Costa et al. (2010) have shown that soil moisture depletion during two partial throughfall exclusion experiments reduced ANPP in old-growth Amazonian forests. Prolonged droughts, usually associated with El Niño events, can result in higher tree mortality in tropical old-growth (Condit et al., 1995; Williamson et al., 2000) as well as regrowth forests (Chazdon et al., 2005). Analogous data from both observational and manipulative studies are lacking for tropical forest regrowth, even though recent estimates indicate that there are ~38 million ha of regrowth in Latin America alone, and the area is growing as unproductive deforested land is abandoned (ITTO, 2002).

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Our primary objective was to investigate the response of ANPP to inter-annual variability in dry-season precipitation and experimentally increased dry-season moisture availability during a 4-year irrigation study. We hypothesized that ANPP would be positively correlated with dry-season precipitation, and that dry-season irrigation would increase ANPP.

2. Material and methods

2.1. Study site

This study was conducted at a field station belonging to the Federal Rural University of Amazonia (U*niversidade Federal Rural da Amazônia* – UFRA), near the city of Castanhal (1° 19′ S, 47° 57′ W) in the state of Pará, Brazil. Since July 2001, daily rainfall was measured 500 m from the experimental area using a standard rain gauge. Prior to July 2001, rainfall data reported here are from the National Agency of Electrical Energy (Agência Nacional de Energia Elétrica – ANEEL) network meteorological station at Castanhal (1° 17′ 53″ S, 47° 56′ 56″ W) located ~3 km from our site, but no longer in operation. There was a strong linear positive relationship between rainfall datasets (R^2 = 0.975) for an overlapping measurement period (10-Sep-2001 to 31-Jan-2002); thus, our rainfall measurements relative to the period prior to July were corrected based on the equation $y = 1.2964x - 0.0595$, where y is site rainfall and x is local rainfall (Castanhal). From 70% to 90% of annual rainfall occurs between January and July, resulting in a dry period from August to December. The number of dry months (rainfall <100 mm month^{-1}) during the experimental period varied from 2 to 5 per year (Table 1).

The soils are classified as Dystrophic Yellow Latosol Stony Phase I (Tenório et al., 1999) in the Brazilian Classification, corresponding to Sombriustox in US Soil Taxonomy. Soil granulometric composition in the first 20 cm is 20% clay, 74% sand, and 6% silt. Concretions represent 16% of the soil volume in the upper 10 cm of soil. In the surface soil (0–10 cm), pH is 5.0, organic carbon (C) is 2.2%, organic C stock is 2.9 kg m^{-2}, total nitrogen (N) is 0.15%, C:N is 14.4, and Mehlich-1 extractable phosphorus is 1.58 mg kg^{-1} (Rangel-Vasconcelos, 2002).

Forest regrowth, annual crops, and active and degraded pastures characterize the landscape surrounding the field station. The stand under study was last abandoned in 1987 following multiple cycles of shifting cultivation, beginning in the 1940s when the old-growth forest was cleared. Each cycle of 1–2 years included cultivation of *Zea mays* L., *Manihot esculenta* Crantz, and *Vigna unguiculata* (L.) Walp, followed by fallow. Typical shifting-cultivation cycles lasted 7–10 years (G. Silva e Souza & O.L. Oliveira personal communication). Trees are mostly evergreen, with a few species (e.g. *Annona paludosa* Aubl. and *Rollinia exsucca* (DC. ex Dunal) A. DC.) showing deciduousness during the dry season. The four most abundant overstorey species are *Lacistema pubescens* Mart., *Myrcia sylvatica* (G. Mey.) DC., *Vismia guianensis* (Aubl.) Choisy and *Cupania scrobiculata* Rich., representing 71% of all stems in the stand. In November 1999, mean stem density for trees with diameter at breast height (DBH) greater than 1 cm at 1.3 m height was 213 individuals per 100 m^2, basal area was 13 m^2 ha^{-1}, average tree height was 4.9 m for the stand (Coelho et al., 2004), and above-ground biomass was 51.5 Mg ha^{-1} for trees with DBH $\geqslant$ 1 cm.

2.2. Experimental design

Treatment plots were established in August 1999, when the forest regrowth was 12 years old. Each treatment plot was 20 × 20 m with a centrally nested 10 × 10-m measurement subplot. There were four replicate plots for the irrigation treatment and four control plots. Adjacent plots were separated by a 10 m buffer strip.

Irrigation was applied at a rate of 5 mm d^{-1}, for about 30 min in the late afternoon, during the dry seasons of 2001–2005. We used rainfall and soil water potential to define approximate boundaries for the dry and wet seasons as described in Vasconcelos et al. (2004). The amount of daily irrigation applied corresponds to regional estimates of daily evapotranspiration for regrowth and old-growth-forest sites in Amazonia (Shuttleworth et al., 1984; Lean et al., 1996; Jipp et al., 1998; Sommer et al., 2002). Irrigation was distributed through tapes with microholes every 15 cm. In 2001, irrigation tapes were spaced 4 m from each other. In the subsequent irrigation periods we reduced the distance between tapes to 2 m to facilitate more even distribution of water. The total amount of irrigation applied ranged from 630 to 790 mm per dry season, representing an increase of 100–200% of water input during the dry-season, and an increase of 21–34% in annual rainfall.

Soil water potential measured with tensiometers (10 cm depth) was significantly higher (less negative) in irrigated than in control plots during the dry season (Vasconcelos et al., 2004). This difference in soil water status between control and irrigated plots was reflected in dry-season differences in soil carbon dioxide efflux (Vasconcelos et al., 2004) and in pre-dawn leaf water potential for an understory species (*Miconia ciliata*) (Fortini et al., 2003).

2.3. Aboveground net primary productivity

Aboveground net primary productivity (ANPP) was estimated as the sum of annual increases in aboveground biomass (AGB) of trees (DBH $\geqslant$ 1 cm) and fine litterfall (Clark et al., 2001a; Grace et al., 2001) between July 2001 and July 2005. To estimate AGB, we used site-specific mixed-species and species-specific allometric equations based on diameter measurements (Ducey et al., 2009); estimated AGB refers to the sum of stemwood, branches, twigs, and foliage biomass. Within each measurement subplot, we measured DBH of every tree with DBH $\geqslant$ 1 cm on an annual basis (every first week of July). Diameter growth was calculated as the annualized increment. Each censused tree was tagged and identified by an experienced field botanist, and voucher specimens were collected for verification at the herbarium of Embrapa Amazonia Oriental

Table 1
Characteristics of rainfall distribution and intensity during the experimental period at the site.

	Measurement interval				
	2000–2001	2001–2002	2002–2003	2003–2004	2004–2005
Annual rainfall (mm)	3060	2214	2647	3241	2622
Minimum monthly rainfall (mm)	66	34	56	42	8
Maximum monthly rainfall (mm)	489	385	499	611	476
Number of dry season months[a]	3	5	4	2[c]	3
Total dry season rainfall (mm)[b]	694	312	400	647	445

[a] Rainfall <100 mm month^{-1}.
[b] Dry season period = August to December.
[c] Not consecutive months.