

Litter dynamics and fine root production in *Schizolobium parahyba* var. *amazonicum* plantations and regrowth forest in Eastern Amazon

Antonio Kledson Leal Silva · Steel Silva Vasconcelos ·
Claudio José Reis de Carvalho · Iracema Maria Castro Coimbra Cordeiro

Received: 8 February 2011 / Accepted: 1 June 2011 / Published online: 15 June 2011
© Springer Science+Business Media B.V. 2011

Abstract Forest plantations and agroforestry systems with *Schizolobium parahyba* var. *amazonicum* have greatly expanded in the Brazilian Amazon, generally as an alternative for reforesting degraded areas. To our knowledge there are no reports of above- and below-ground production in these forest systems. We quantified litter and fine root production in 6-yr old *Schizolobium*-based plantation forests (monospecific: MON, mixture: MIX, and agroforestry system: AFS) and in ~25-yr old regrowth forest (REG) over 8–12 months. We used litter traps and ingrowth cores to quantify litter and fine root production, respectively. Annual litter production was significantly lower in *Schizolobium*-based plantations (mean \pm standard error, MON=5.92 \pm 0.15, MIX=6.08 \pm 0.13, AFS=6.63 \pm 0.13 Mg ha⁻¹ year⁻¹) than in regrowth forest (8.64 \pm 0.08 Mg ha⁻¹ year⁻¹). *Schizolobium*-based plantations showed significantly higher litter stock

(MON=7.7 \pm 1.0, MIX=7.4 \pm 0.1 Mg ha⁻¹) than REG (5.9 \pm 1.3 Mg ha⁻¹). Total fine root production over an 8-month period was significantly higher in *Schizolobium*-based plantations (MON=3.8 \pm 0.2, MIX=3.4 \pm 0.2, AFS=2.7 \pm 0.1 Mg ha⁻¹) than in REG (1.1 \pm 0.03 Mg ha⁻¹). Six-yr old *Schizolobium*-based plantations and ~25-yr old regrowth forests showed comparable rates of litter + fine root production, suggesting that young forest plantations may be an interesting alternative to restore degraded areas due to early reestablishment of organic matter cycling under the studied conditions.

Keywords Amazon · Decomposition · Litter · Fine root · Regrowth forest

Introduction

Litter and fine root production are major processes involved in nutrient cycling (Vitousek and Sanford 1986; Nadelhoffer and Raich 1992). Thus, changes to the natural patterns of litter and fine root production may have substantial impacts on ecosystem functioning. In the Brazilian Amazon, forest conversion to cattle pasture or agriculture have greatly modified the natural patterns of litter and fine root production, usually leading to land degradation (Luizão et al. 2006).

Forest regrowth after abandonment of cattle pasture and slash-and-burn agriculture plays an important role in reestablishing carbon and nutrient cycling through litter and fine root dynamics (Nepstad et al. 2001;

Responsible Editor: Johannes Lehmann.

A. K. L. Silva
Universidade Federal do Para, Programa de Pos-graduacao
em Ciencias Ambientais,
Belem, Para, Brazil

S. S. Vasconcelos (✉) · C. J. R. de Carvalho
Embrapa Amazonia Oriental,
Laboratorio de Ecofisiologia Vegetal,
Belem, Para, Brazil
e-mail: steel@cpatu.embrapa.br

I. M. C. C. Cordeiro
Tramontina Belem S.A.,
Belem, Para, Brazil

Davidson et al. 2007). In addition, forest regrowth often represent an important source of income (woody and nonwoody forest products) to local people (Brown and Lugo 1990). Adequate management of forest regrowth can represent an important alternative to reduce pressure on old-growth forest sites and restore degraded areas in the Amazon region.

Plantation forests and agroforestry systems have been suggested as viable alternatives for restoring degraded areas since they can provide forest products (wood, firewood) as well as ecological benefits, such as improved nutrient cycling, soil conservation, and recovery of biodiversity (Lamb et al. 2005; Montagnini et al. 2006). In the Brazilian Amazon, *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby is one of the most important planted native tree species, with wide use in the plywood industry. *S. parahyba* is a large-size tree of the Leguminosae family (sub-family Caesalpinacea) and naturally occurs in primary and successional upland and high floodplain forest ecosystems in the Brazilian Amazon (Ducke 1949).

Due to its fast growth and relatively tolerance to low soil fertility, this species has been frequently planted in degraded areas (Gazel Filho et al. 2007). The relative simplicity of *S. parahyba* silviculture has also made it attractive for use in commercial-scale reforestation, as well as in agroforestry systems. The area planted with *S. parahyba* increased from 79,159 ha in 2007 to 85,320 ha in 2009 in the Brazilian Amazon (ABRAF 2010).

In spite of the rapid expansion of *S. parahyba* plantation forests in the Brazilian Amazon over the last few years, to our knowledge there are no reports of above- and below-ground productivity in these forestry systems. This information is necessary to understand the mechanisms through which *S. parahyba* plantation forests may contribute to restore degraded areas in comparison to forest regrowth. Therefore, in this study we compared litterfall and fine root production in *S. parahyba* plantation forests and regrowth forest.

Materials and methods

Study area

This study was carried out in an experimental field belonging to the Tramontina Belém S.A. company (Tramontina Ranch), located in the municipality of

Aurora do Pará (2°10'S, 47°34'W), northeastern of the State of Pará. The predominant soils of the study area are sandy-clay Yellow Latosol (Brazilian Soil Taxonomy) (Cordeiro 2007), corresponding to Oxisol in US Soil Taxonomy. We selected three 6-yr old plantation forest sites based on *Schizolobium parahyba* var. *amazonicum* (hereafter called *Schizolobium*-based plantations): a monospecific plantation (MON), a mixture with *Cordia goeldiana* Huber (Boraginaceae) (MIX), and an agroforestry system with *C. goeldiana* and *Ananas comosus* var. *erectifolius* (Bromeliaceae) (AFS). Within-row and between-row spacing were 4 m and 3 m for tree species and 0.5 m and 0.8 m for *A. comosus*. We also selected a ~25-yr old regrowth forest ecosystem (REG) for comparison purposes.

Before the establishment of the forest plantations in 2002, the area was covered with abandoned and degraded pasture (mostly *Brachiaria humidicola*). Cattle manure (500 g hole⁻¹) and chicken coop straw (150 g hole⁻¹) were applied at planting. *A. comosus* was planted in 2007 and its leaves were not harvested during the study. In a plant survey carried out in November 2007, 172 trees of 26 species were identified in 4 30 m×30 m-plots in the regrowth forest, where the most predominant species were *Casearia arborea*, *Tapirira guianensis*, *Abarema cochleata* and *Lecythis lurida*.

According to data obtained from a meteorological station located about 2 km from the study area, total rainfall was 2,200 mm, average annual temperature was 26°C, and relative humidity was 74% in 2007. During the experimental period, from October 2007 to September 2008, total rainfall was 2,658 mm. Accumulated rainfall from December 2007 to May 2008 was 82% of the annual rainfall; this period was considered as the rainy season in the context of this study. During the dry season (October to November 2007 and June to September 2008) 5 months had monthly rainfall less than 100 mm, a limit which characterizes the dry season in related studies in the Amazon (Sombroek 2001).

We established four plots per forest type each measuring 20 m×20 m for plantations and 30 m×30 m for secondary forest. There is no true replication because we could not find other forest stands with the same age, management, and soil conditions. We acknowledge that pseudo-replications can be a limitation of our study, as in many other published studies related to litter and fine root production.

In September 2008, soil samples were collected with a hand auger from each forest type at depths of 0–10 cm and 10–20 cm for chemical and physical analyses (Table 1). One composite sample made up of 12 cores from each depth per forest type was analyzed at the Soil Laboratory of Embrapa Amazonia Oriental. Soil pH, total phosphorus, exchangeable potassium, and exchangeable calcium levels (Table 1) were lower compared with levels defined as adequate for the State of Pará (Cravo et al. 2007).

Stem biomass

Diameter at breast height (Dbh) and height (H) of *S. parahyba* and *C. goeldiana* trees (Table 1) were measured in October 2008 for the plantation treatments, except for the MIX treatment, when unforeseen cutting in September 2008 made measurements

impossible. In November 2007 we measured Dbh of all trees with $\text{Dbh} \geq 5$ cm in the regrowth forest. We used allometric equations (Table 1) based on Dbh to estimate aboveground biomass for each treatment.

Litter production, stock, and turnover

Three litter traps each with a 1 m² internal area were installed in each plot. Weekly collections were carried out from October 2007 to September 2008. Samples for the *Schizolobium*-based plantations were separated into fractions of (a) *S. parahyba* leaflets, (b) *S. parahyba* rachis, (c) *C. goeldiana* leaves, (d) reproductive material (flowers, fruits, seeds) + miscellanea (fragments of unclassified litter in the remaining fractions), (e) fine branches (diameter ≤ 1 cm), and (f) coarse branches (diameter > 1 cm). During the experimental period, we did not encounter any *A.*

Table 1 Stand (diameter at breast height—Dbh, height—H, density and aboveground biomass) and soil characteristics in the experimental plots evaluated in 6-yr old *Schizolobium parahyba* var. *amazonicum*-based plantation forests (MON:

monospecific, MIX: mixture, AFS: agroforestry system) and in 25-yr old regrowth (REG) forest in eastern Amazon, Brazil. Stand data are average \pm standard error ($n=4$)

Parameter	Forest type			
	MON	MIX	AFS	REG
Vegetation				
Dbh (cm)	16.55 \pm 0.46 (<i>S. parahyba</i>)	17.31 \pm 0.25 (<i>S. parahyba</i>) 10.38 \pm 0.48 (<i>C. goeldiana</i>)	–	9.38 \pm 0.48
H (m)	16.80 \pm 2.38 (<i>S. parahyba</i>)	15.97 \pm 0.59 (<i>S. parahyba</i>) 10.02 \pm 0.86 (<i>C. goeldiana</i>)	–	–
Density (Individual ha ⁻¹)	878 (<i>S. parahyba</i>)	733 (<i>S. parahyba</i>) 222 (<i>C. goeldiana</i>)	–	3583
Biomass (Mg ha ⁻¹)	55.3 \pm 3.5 ⁽¹⁾	64.3 \pm 2.1 ⁽²⁾	–	56.6 \pm 20.1 ⁽³⁾
Soil (0–20 cm depth)				
pH	5.15	5.15	5.05	5.00
Organic matter (g kg ⁻¹)	10.1	13.1	14.3	11.5
Total P (mg dm ⁻³)	2.5	3.0	3.5	1.5
Exchangeable K (mg dm ⁻³)	16	17	18	22
Exchangeable Ca (cmol _c dm ⁻³)	0.75	1.10	0.85	0.90
Sand (%)	90	88	84	84
Silt (%)	3	4	5	6
Clay (%)	7	8	11	10
Textural class	Sandy	Sandy	Sandy	Sandy
Bulk density (g cm ⁻³)	1.49	1.47	1.49	1.45

⁽¹⁾ Allometric equation for *Schizolobium parahyba*: Biomass = 0.076 × (Dbh^{2.346}) (Vasconcelos, personal communication)

⁽²⁾ Allometric equation for *Cordia goeldiana*: Biomass = Exp(−1.754 + 2.665 × ln(Dbh)) × 0.6 (Higuchi et al. 1998)

⁽³⁾ Allometric equation for regrowth forest ecosystem: ln(Biomass) = −1.9968 + 2.4128 × ln(Dbh) (Nelson et al. 1999)

comosus leaf litterfall. In the regrowth forest, litter was separated into fractions of (a) leaves, (b) reproductive material + miscellanea, (c) fine branches, and (d) coarse branches. After separation, samples were oven-dried at 60–70°C for 72 h and weighed to a precision of 0.01 g.

Litter stock was measured during the rainy (March) and dry (August) seasons. In each season, five randomly selected samples were collected per plot using a 0.5 m×0.5 m metallic frame. In the laboratory, soil particles were removed from the samples manually which were then separated into three fractions: (1) *S. parahyba* leaflets, *C. goeldiana* leaves, understorey leaves, flowers, fruits, miscellanea, and fine branches; (2) *S. parahyba* rachis; and (3) coarse branches, where the sum of (1) and (2) was equivalent to non-woody litter. In the regrowth forest, litter stock was separated into (1) leaves, flowers, fruit, miscellanea, and fine branches, corresponding to the non-woody litter; and (2) coarse branches. Samples were dried and weighed in the same manner as was litter production. There were two manual weedings using hand hoes in the area where the AFS treatment plots were established, one in January and the other in July 2008, both just a few weeks before litter collections. Since weeding clearly disturbed litter layer, we could not report litter stock data for the AFS treatment plots.

The litter turnover rate was estimated with an equation proposed by Olson (1963): $k = L/X$, where k is the turnover rate (yr^{-1}), L is annual litter production ($\text{g m}^{-2} \text{ year}^{-1}$), and X is ground litter stock (g m^{-2}). One limitation of this equation is the assumption of steady state (litter inputs = litter losses) (Olson 1963), which may not be valid for young forests.

Fine root production

We used the ingrowth core technique to estimate fine root (diameter ≤ 2 mm) production down to 10 cm soil depth (Lima et al. 2010). The ingrowth bags were filled with root-free dry soil. The average density of the resulting soil in the growth bags was $0.76 \pm 0.01 \text{ g cm}^{-3}$, which was 54.3% less than the soil density (0–10 cm) determined by the volumetric ring method (Embrapa 1997) in the first semester of 2008, in the same experimental plots of this study (1.4 ± 0.01 , 1.5 ± 0.00 , 1.4 ± 0.07 and $1.4 \pm 0.05 \text{ g cm}^{-3}$ for MON, MIX, AFS, and REG, respectively) (Dias 2008). Five cylindrical bags (10 cm-high by 5.5 cm-diameter)

made of polyethylene (2 mm×3 mm mesh size) were installed randomly in each plot, resulting in 20 bags per forest type.

Five samples were removed every 2 months from February to September 2008 and replaced with new bags with rootless soil; replacement bags were installed into the same holes. The root separation procedure involved washing samples with running water in two different sieves with 2 mm and 1 mm mesh. Next, we used forceps to separate live (biomass) and dead (necromass) fine roots based on appearance, texture, color, and elasticity features (Válverde-Barrantes et al. 2007). Live and dead roots were oven-dried at 65°C for 48 h and weighed to a precision of 0.0001 g.

The intra-annual temporal variability of total fine root and litter production in each treatment was calculated according to the equation $[(\text{Max} - \text{Min})/\text{Max}] \times 100$, where Max = maximum monthly production and Min = minimum monthly production.

Statistical analysis

The 9.0 version of the SAS program was used for statistical analysis (SAS 2004). The PROC MIXED procedure was used to test the effects of treatment, date, and the interaction between treatment and date on litter production, litter stock, and fine root production, using a repeated measures analysis of variance (Littell et al. 1998). When necessary, data were natural log transformed to meet normality and homocedasticity requirements. Tables and figures show averages and standard errors of the non-transformed data. The CONTRAST procedure was used to test if litter production was affected significantly by the dry and rainy seasons. The PROC ANOVA procedure was used to test the effect of treatments on litter stock turnover rate (k) values. Treatment means were compared using the Tukey test at a level of $P < 0.05$.

Results

Litter production

Annual non-woody and reproductive + miscellanea litterfall were significantly higher for the regrowth forest (REG) than for *Schizolobium*-based plantations, except for the AFS (Table 2). Leaf litterfall did not

Table 2 Litter production, stock, and turnover rate of 6-yr *Schizolobiumparahyba*-based plantations (MON: monoespecific, MIX: mixture, AFS: agroforestry system) and 25-yr old regrowth forest (REG) in eastern Amazonia (data are average \pm standard error, $n=12$). Different superscript letters indicate statistically significant differences between treatments ($P<0.05$, Tukey's test). Non woody is the sum of leaves, reproductive + miscellanea, and fine woody fractions. Litter stock data are the average of wet and dry season samples

Fraction	Litter production ($\text{Mg ha}^{-1} \text{ year}^{-1}$)			
	MON	MIX	AFS	REG
Total leaves	5.61 \pm 0.15 ^a	5.54 \pm 0.13 ^a	6.12 \pm 0.13 ^a	6.11 \pm 0.08 ^a
<i>S. parahybaleaflets</i>	4.61 \pm 0.12 ^{ab}	4.18 \pm 0.09 ^b	4.84 \pm 0.10 ^a	–
<i>S. parahybarachis</i>	1.00 \pm 0.03 ^a	0.78 \pm 0.03 ^a	0.90 \pm 0.02 ^a	–
<i>C.goeldianaleaves</i>	–	0.58 \pm 0.02 ^a	0.38 \pm 0.01 ^a	–
Reproductive + miscellanea	0.27 \pm 0.01 ^b	0.43 \pm 0.01 ^b	0.44 \pm 0.01 ^{ab}	1.55 \pm 0.02 ^a
Fine branches	0.04 \pm 0.00 ^c	0.11 \pm 0.00 ^b	0.06 \pm 0.00 ^{bc}	0.98 \pm 0.01 ^a
Non-woody	5.92 \pm 0.15 ^b	6.08 \pm 0.13 ^b	6.63 \pm 0.13 ^{ab}	8.64 \pm 0.08 ^a
Fraction	Litter stock (Mg ha^{-1})			
	MON	MIX	–	REG
Non-woody	7.54 \pm 1.05 ^a	7.20 \pm 0.02 ^a	–	4.52 \pm 1.03 ^b
Rachis	2.35 \pm 0.05 ^a	1.85 \pm 0.10 ^b	–	–
Fraction	Turnover rate (yr^{-1})			
	MON	MIX	–	REG
Non-woody	0.79 \pm 0.02 ^b	0.85 \pm 0.05 ^b	–	1.90 \pm 0.10 ^a

differ significantly among treatments. The regrowth forest showed significantly higher fine branch litterfall than the treatments including *Schizolobium* (Table 2).

S. parahyba leaflets represented between 69% and 76% of total annual litter production in treatments MON, MIX, and AFS. The sequence of the most to the least representative fractions was (a) leaflets \gg rachis $>$ *Cordia* leaves $>$ reproductive + miscellanea \gg fine branches for MIX and AFS, (b) leaflets \gg rachis $>$ reproductive + miscellanea \gg fine branches for MON, and (c) leaves \gg reproductive + miscellanea $>$ fine branches for REG (Table 2).

Litter production was significantly higher during the dry season than in the rainy season for leaves ($P=0.0019$) and non-woody ($P<0.001$) fractions. *Schizolobium*-based plantations showed significantly higher litterfall (leaves and non-woody) than the regrowth forest only during the dry season (August 2008) (Fig. 1).

The intra-annual temporal variability of non-woody litter production in each treatment was greater for MON (94.5%), MIX (93.4%), and AFS (91.9%) than for REG (62.1%).

Litter stock and turnover

Mean annual non-woody litter stock was significantly lower in regrowth forest (REG) than in

Schizolobium-based plantations (MON and MIX), but there was no significant difference between MON and MIX (Table 2). For the MON and REG forests, non-woody litter stock was significantly higher in the rainy season (MON=8.6 \pm 0.4, REG=5.6 \pm 0.4 Mg ha^{-1}) than in the dry season (MON=6.5 \pm 0.4, REG=3.5 \pm 0.3 Mg ha^{-1}). For the MIX treatment, there was no significant difference in non-woody litter stock between sampling dates (rainy season = 7.2 \pm 0.3, dry season = 7.2 \pm 0.5 Mg ha^{-1}). Rachis litter stock was significantly greater in MON than in MIX for both sampling dates.

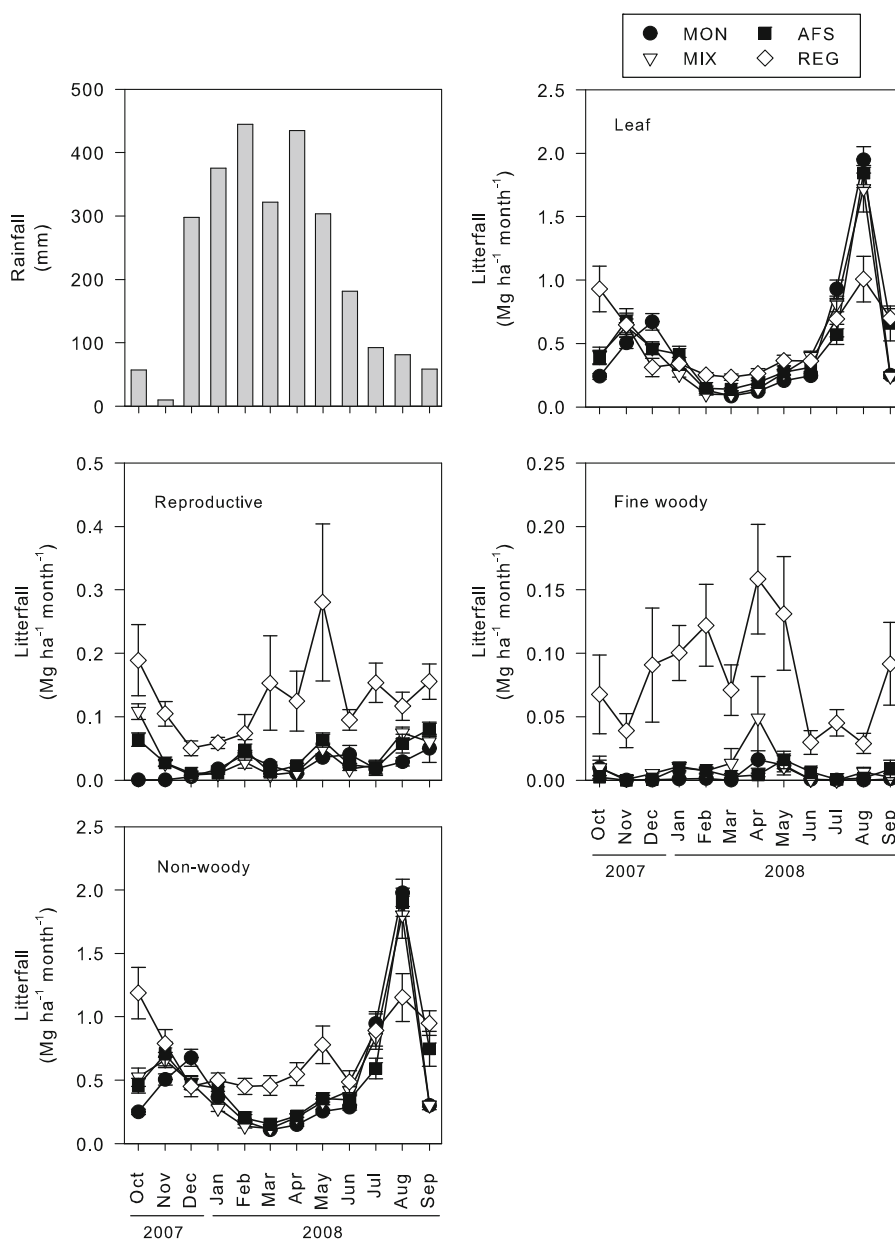
The REG ecosystem showed significantly higher non-woody litter stock turnover rates ($P<0.001$) than the MON and MIX treatments (Table 2).

Fine root production

Total fine root production over the evaluation period (8 months) was significantly higher ($P<0.05$) in *Schizolobium*-based plantations (mean \pm standard error, MON=380.3 \pm 20.6 g m^{-2} , MIX=343.0 \pm 18.4 g m^{-2} , AFS=265.5 \pm 9.9 g m^{-2}) than in REG (107.2 \pm 2.7 g m^{-2}). The production of live roots varied between 98.1% and 99.4% of the measured total for the *Schizolobium*-based treatments, while the regrowth forest showed 96.6% of live roots.

Bi-monthly root production was significantly affected by the interaction between treatment and

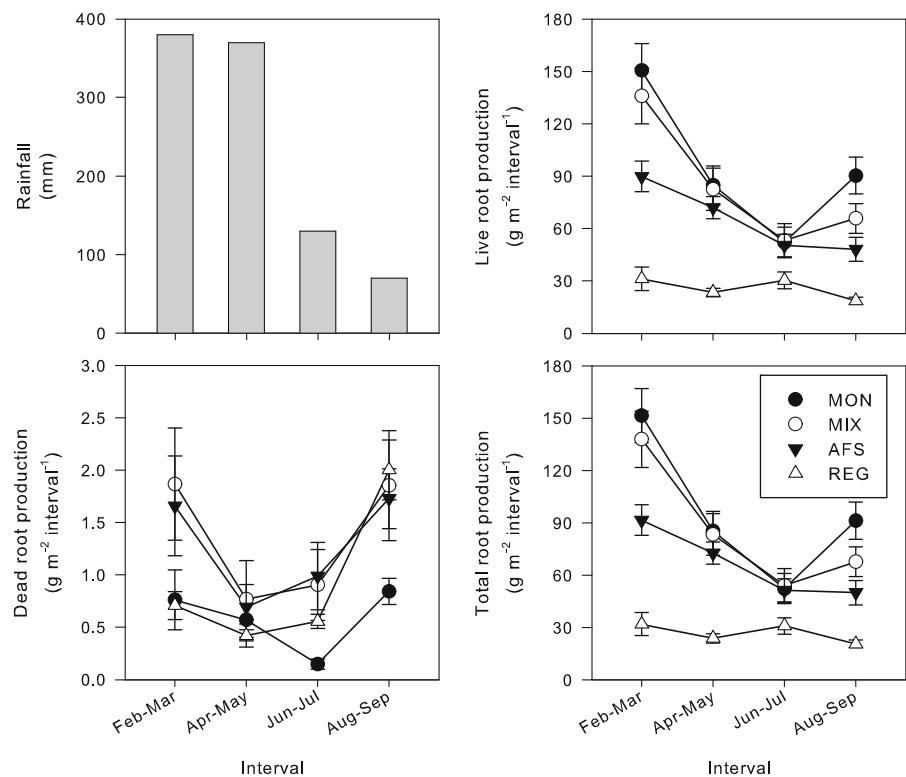
Fig. 1 Monthly rainfall and litter production in 6-yr old *Schizolobium parahyba* var. *amazonicum*-based plantations (MON: monospecific, MIX: mixture, AFS: agro-forestry system) and 25-yr old regrowth forest (REG) in eastern Amazon, Brazil. Litter production data are average \pm standard error ($n=12$)



measurement interval for live and total roots. For MON and MIX, fine root production decreased from the first (rainy season) to the third measurement (dry season) intervals, with no statistical difference between the third and the last intervals. Live and total fine root production showed the same trend in the AFS forest. Root mortality was significantly affected by treatment only, with higher mortality for MIX ($5.4 \pm 0.3 \text{ gm}^{-2}$), AFS ($5.1 \pm 0.3 \text{ gm}^{-2}$), and REG ($3.7 \pm 0.4 \text{ gm}^{-2}$) than for MON ($2.3 \pm 0.2 \text{ gm}^{-2}$).

Bi-monthly variation in total root production (live and dead) in each treatment was most evident in treatments MON (65%), MIX (61%), and AFS (46%) when compared to the regrowth forest (35%). Total and live fine root production in *Schizolobium*-based plantation forests decreased during the rainy season, with further reduction in the dry season (Fig. 2). The successional forest had the lowest production of live and live+dead fine root for the whole study period (Fig. 2).

Fig. 2 Rainfall and accumulated fine root production of 6-yr *Schizolobium parahyba*-based plantations (MON: monoespecific, MIX: mixture, AFS: agroforestry system) and 25-yr old regrowth forest (REG) in eastern Amazon, Brazil. Data are average \pm standard error ($n=20$)



Discussion

Litter production, stock, and turnover

Annual non-woody litter production in the regrowth forest ecosystem (REG) ($8.64 \pm 0.08 \text{ Mg ha}^{-1} \text{ year}^{-1}$) is towards the upper end of the range of variation (4.9 to $9.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$) of litter production in tropical regrowth forest ecosystems and close to that of primary forest ecosystems (Cuevas and Medina 1986; Cuevas et al. 1991; Lugo 1992; Martius et al. 2004; Vasconcelos et al. 2004). Non-woody litter production (5.92 to $6.63 \text{ Mg ha}^{-1} \text{ year}^{-1}$) in *Schizolobium*-based plantations can be considered high in comparison with forest plantations in the Amazon and in other tropical regions (Lugo 1992; Smith et al. 1998; Barlow et al. 2007). In fact, large variation (3.1 to $14.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$) is observed in mono and multispecific forest plantations in the Amazon and other tropical regions (Lugo 1992; Cuevas and Lugo 1998; Martius et al. 2004). These variations are likely related to differences in species composition, stand age, soil, and climate.

Litterfall seasonality observed in this study is consistent with results commonly reported for forest

ecosystems in the Amazon and other tropical regions (Barlow et al. 2007; Smith et al. 1998; Vasconcelos et al. 2004; Chave et al. 2010), i.e., litterfall was higher in the dry season than in the wet season. Litterfall seasonality throughout year was lower for regrowth forest than for *Schizolobium*-based plantations. High leaf fall rates found in *Schizolobium*-based plantations during the dry season probably reflect a strategy of the dominant species (*S. parahyba*) to tolerate water stress. Leaf fall reduces the evapotranspiration area, therefore mitigating water stress (Borchert et al. 2002).

Factors such as climate, soil, species composition, and plantation age, as well as the litter decomposition rate of each species, control litter accumulation (Lugo 1992; Martius et al. 2004). *Schizolobium*-based plantations showed higher litter stock than regrowth forest, consistent with related studies in the tropics (Cuevas et al. 1991; Lugo 1992; Smith et al. 1998; Martius et al. 2004). Despite higher litterfall, regrowth forest showed lower litter stock due to higher turnover rates than *Schizolobium*-based plantations. Further investigation is needed to clarify the factors that control litter turnover rates in regrowth and *Schizolobium*-based plantation forests. It is likely that

differences in canopy cover that affect microclimate in these ecosystems may play an important role in controlling litter decomposition.

Fine root production

We found higher fine root production in the planted forests than in the regrowth forest, which is different to related studies in the tropics (Cuevas et al. 1991; Smith et al. 2002). The larger live root mass accumulated during the study period in *Schizolobium*-based plantations is consistent with likely high demand for water and soil nutrients to cope with the high growth rates of this species. With the same methodology used here, Lima et al. (2010) reported annual fine root production of 0.86 Mg ha⁻¹ year⁻¹ for a ~20-yr old regrowth forest in eastern Amazon, which is close to our estimate (1.07 Mg ha⁻¹ year⁻¹) for the successional site.

We did not find a clear relationship between fine root production and rainfall variation for both *Schizolobium*-based plantations and regrowth forest. During the measurement period total fine root production in the *Schizolobium*-based plantations decreased from 20% to 44% towards the second half of the wet season, despite a minimal reduction in rainfall (< 3%) over this period. Fine root production further declined with the onset of the dry season, when bi-monthly rainfall decreased 65%. Thus, the observed decrease in fine root production could not be readily associated with rainfall variation in this study. Other factors such as tree phenology or understory species may have affected fine root production at our site. We noted that grasses—which usually show high fine root productivity—dominated the understory of the MON and MIX treatments during the wet period; due to more frequent weeding

we did not observe much grasses in the agroforestry system.

Fine root production in the regrowth forest did not vary significantly through time despite great rainfall variation during the experimental period. Other studies have shown that fine root production may vary with rainfall seasonality in the Brazilian Amazon, but results do not agree with respect to patterns of root responses to rainfall. Lima et al. (2010) found greater fine root production in the dry season than in the wet season in a regrowth forest in eastern Amazonia. On the other hand, Metcalfe et al. (2008) observed a reduction in fine root production during transition from the rainy to the dry season in an upland old-growth forest in the National Caxiuanã Forest, Brazil.

Higher litter production and decomposition rates in the regrowth forest may have resulted in increased nutrient mineralization in relation to the *Schizolobium*-based plantations. Thus the need to invest in fine roots to increase nutrient uptake may have been lower for the regrowth forest, which is consistent with our observations of lower production of fine root for this ecosystem over the course of the experiment.

Although plantation and regrowth forests had different rates of annual production of litter and fine roots, they showed comparable rates when we summed annual litter and fine root production (Table 3). These results show the importance of belowground evaluation in comparative biomass production studies.

Plantations showed greater seasonality of litter and fine root production than regrowth forest, consistent with previous studies in tropical forests (Smith et al. 1998; Lugo 1992). These results may have important implications to forest simplification effects on global change feedbacks, especially if

Table 3 Organic matter input from litter and fine root production in 6-yr old *Schizolobium parahyba*-based plantations (MON: monoespecific, MIX: mixture, AFS: agroforestry

system) and 25-yr old regrowth (REG) forest in eastern Amazonia (data are average ± standard error, n=4)

Forest type	Total litter production Mg ha ⁻¹ 18 month ⁻¹	Fine root production	Total litter + fine root production
MON	4.22±0.46	3.80±0.21	8.02±0.41
MIX	4.15±0.41	3.43±0.18	7.58±0.31
AFS	4.57±0.52	2.66±0.10	7.22±0.45
REG	5.86±0.23	1.07±0.03	6.93±0.20

greater inherent production seasonal variability renders forest plantation functional processes more vulnerable to extreme climatic events.

We acknowledge that pseudo-replication is a limitation of this study and as such our results should be viewed with caution. Six-year old *Schizolobium parahyba* plantations reestablished litterfall rates close to those found in the 25-yr old regrowth forest. Overall, plantations and regrowth forest showed similar estimated above and belowground production. Our results suggest that *Schizolobium parahyba* plantation forests may be an interesting alternative to forest regrowth to restore degraded areas due to their high capacity to stock litter and produce superficial fine roots.

Acknowledgments We thank Guilherme Cordeiro for his logistical support and Thiago Sozinho, Carolina Shizue, and Aline Faria, for their field and laboratory assistance. We also thank two anonymous reviewers for insightful comments that improved the manuscript. Fellowship financing was made available to Silva by Coordenacao de Aperfeicoamento de Pessoal de Nivel Superior (CAPES), as this study was part of the requirements necessary for obtaining a Master's Degree in the post-graduate Environmental Studies Program of the Universidade Federal do Para. This study was partly funded by Project Carboagro.

References

- ABRAF (2010) Anuario estatístico da ABRAF 2010 ano base 2009. Associação Brasileira de Produtores de Florestas Plantadas, Brasília
- Barlow J, Gardner TA, Ferreira LV, Peres CA (2007) Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. *Forest Ecol Manag* 247:91–97
- Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34(1):27–39
- Brown S, Lugo AE (1990) Tropical secondary forests. *J Trop Ecol* 6:1–32
- Chave J, Navarrete D, Almeida S, Álvarez E, Aragão LEOC, Bonal D, Châtelet P, Silva-Espejo JE, Goret JY, von Hildebrand P, Jiménez E, Patiño S, Peñuela MC, Phillips OL, Stevenson P, Malhi Y (2010) Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences* 7(1):43–55. doi:10.5194/bg-7-43-2010
- Cordeiro IMC (2007) Comportamento de *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby e *Ananas comosus* var. *erectifolius* (L. B. Smith) Coppens & Leal sob diferentes sistemas de cultivo no município de Aurora do Pará (PA). Dissertation, Universidade Federal Rural da Amazônia, Belém
- Cravo MDS, Viégas IDJM, Brasil EC (2007) Recomendacoes de adubacao e calagem para o estado do Para. Embrapa Amazonia Oriental, Belém
- Cuevas E, Medina E (1986) Nutrient dynamics within Amazonian forest ecosystems I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia* 68:466–472
- Cuevas E, Lugo AE (1998) Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. *Forest Ecol Manag* 112(3):263–279
- Cuevas E, Brown S, Lugo AE (1991) Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. *Plant Soil* 135:257–268
- Davidson EA, de Carvalho CJR, Figueira AM, Ishida FY, Ometto JPHB, Nardoto GB, Saba RT, Hayashi SN, Leal EC, Vieira ICG, Martinelli LA (2007) Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447 (7147):995–998. doi:http://www.nature.com/nature/journal/v447/n7147/suppinfo/nature05900_S1.html
- Dias JD (2008) Dinamica do amonio e nitrato em solos consorciados com plantios de parica (*Schizolobium amazonicum*) em Aurora do Para, Para. Thesis, Universidade Federal do Para Belém
- Ducke A (1949) Notas sobre a flora neotropica II: as leguminosas da Amazonia brasileira. *IAN Boletim Tecnico* 18. Belém
- Embrapa (1997) Manual de metodos de analise de solo, 2nd edn. EMBRAPA-CNPS, Rio de Janeiro
- Gazel Filho AB, Cordeiro IMCC, Alvarado JR, Santos Filho BGD (2007) Producao de biomassa em quatro procedencias de parica (*Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby no estadio de muda. *Rev Brasil Bioci* 5:1047–1049
- Higuchi N, Santos J, Ribeiro RJ, Minette L, Biot Y (1998) Biomassa da parte aerea da vegetacao da floresta tropical umida de terra-firme da Amazonia brasileira. *Acta Amazonica* 28(2):153–166
- Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. *Science* 310 (5754):1628–1632. doi:10.1126/science.1111773
- Lima TTS, Miranda IS, Vasconcelos SS (2010) Effects of water and nutrient availability on fine root growth in eastern Amazonian forest regrowth, Brazil. *New Phytol.* doi:10.1111/j.1469-8137.2010.03299.x
- Littell RC, Henry PR, Ammerman CJ (1998) Statistical analysis of repeated measures data using SAS procedures. *J Anim Sci* 76:1216–1231
- Lugo AE (1992) Comparison of tropical tree plantations with secondary forests of similar age. *Ecol Monogr* 62 (1):1–41
- Luizão FJ, Tapia-Coral S, Gallardo-Ordinola J, Silva GC, Luizão RC, Trujillo-Cabrera L, Wandelli E, Fernandes ECM (2006) Ciclos biogeoquímicos em agroflorestas da Amazonia. In: Gama-Rodrigues ACd, Barros NFd, Gama-Rodrigues Efd et al. (eds) *Sistemas agroflorestais: bases científicas para o desenvolvimento sustentável*. Embrapa Informacao Tecnológica, Brasília, pp 87–100

- Martius C, Höfer H, Garcia MVB, Römbke J, Hanagarth W (2004) Litter fall, litter stocks and decomposition rates in rainforest and agroforestry sites in central Amazonia. *Nutr Cycl Agroecosyst* 68:137–154
- Metcalf DB, Meir P, Aragao LEOC, Costa ACL, Braga AP, Gonçalves PHL, Silva Junior JA, Almeida SS, Dawson LA, Malhi Y, Williams M (2008) The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant Soil* 311:189–199
- Montagnini F, Cusack D, Petit B, Kanninen M (2006) Environmental services of native tree plantations and agroforestry systems in Central America. In: Montagnini F (ed) *Environmental services of agroforestry systems*. Food Products Press, Binghamton, pp 51–67
- Nadelhoffer KJ, Raich J (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology* 73(4):1139–1147
- Nelson BW, Mesquita R, Pereira JLG, Souza SGAD, Batista GT, Couto LB (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecol Manag* 117:149–167
- Nepstad D, Moutinho PRS, Markewitz D (2001) The recovery of biomass, nutrient stocks, and deep soil functions in secondary forests. In: McClain ME, Victoria RL, Richey JE (eds) *The biogeochemistry of the Amazon basin*. Oxford University Press, New York, pp 139–155
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331
- SAS (2004) *SAS/STAT® 9.1 User's Guide*. SAS Institute Inc., Cary
- Smith CK, Oliveira FDA, Gholz HL, Baima A (2002) Soil carbon stocks after forest conversion to tree plantations in lowland Amazonia, Brazil. *Forest Ecol Manag* 164:257–263
- Smith K, Gholz HL, Oliveira FDA (1998) Litterfall and nitrogen-use efficiency of plantations and primary forest in the eastern Brazilian Amazon. *Forest Ecol Manag* 109:209–220
- Sombroek W (2001) Spatial and temporal patterns of Amazon rainfall. Consequences for the planning of agricultural occupation and the protection of primary forests. *R Swed Acad Sci* 30(7):388–396
- Válverde-Barrantes OJ, Raich JW, Russell AE (2007) Fine-root mass, growth and nitrogen content for six tropical tree species. *Plant Soil* 290:357–370
- Vasconcelos SS, Zarin DJ, Capanu M, Littell R, Davidson EA, Ishida FY, Santos EB, Araújo MM, Aragão DV, Rangel-Vasconcelos LGT, Oliveira FDA, McDowell WH, Carvalho CJRD (2004) Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Global Biogeochem Cycles* 18:GB2009, doi:[2010.1029/2003GB002210](https://doi.org/10.1029/2003GB002210)
- Vitousek PM, Sanford RL, Jr. (1986) Nutrient cycling in moist tropical forest. *Annu Rev Ecol Syst* 17:137–167