Leaf area index and root biomass variation at different secondary forest ages in the eastern Amazon

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ABSTRACT

In the Amazon region, small farmers use secondary forests as the only source of nutrients for agriculture, performing slash and burn in a rotation system. Secondary forests cover a large area of these landscapes and are crucial to maintaining soil fertility. The main objectives of this study were to gain insight into the seasonal variations in leaf area index (LAI) and root biomass growth, and to improve the accuracy of carbon sequestration estimates in early successional tropical secondary forests following shifting cultivation. Secondary vegetation of three different ages (1 year, 6 years and 10 years after shifting cultivation) were monitored monthly with a LI-COR Plant Canopy Analyzer, and root growth was seasonally measured down to a depth of 400 cm using ingrowth bags. The youngest secondary forests showed strong LAI seasonality, and the seasonality in LAI decreased in the oldest forest. The roots grew throughout the year even though the growth rates were higher during the dry season, which supported a dense biomass of leaves over the year. This study clearly indicates that information on deep rooting and seasonality of leaf area in secondary tropical forests is essential for understanding ecosystem ecophysiology, as well as community ecology and biogeochemical cycles.

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1. Introduction

The biomass of tropical forests plays an important role in the global carbon cycle, both as a dynamic pool of carbon and as a source of carbon dioxide to the atmosphere in areas suffering deforestation (Malhi et al., 2006). In the northeast area of the Brazilian Amazon, distinct effects of forest conversion to other land uses have already been observed, with implications for carbon storage. This region has been undergoing a change for over one hundred years and is dominated by small-scale farmers performing swidden (slash-and-burn) agriculture (Vieira, 1996). This management practice consists of a two-year agricultural period interspersed with three- to eight-year fallow periods. The land preparation, performed with fire, results in a significant amount of carbon emissions to the atmosphere (Sommer et al., 2000; Nepstad et al., 2001; Fearnside et al., 2007). Nonetheless, during the fallow period the secondary vegetation regenerates from the remaining stems and roots (Uhl et al., 1988; Tucker et al., 1998), producing a mosaic of secondary forests of different ages.

Fallows with secondary vegetation are effective tools for agricultural productivity recovery, through the accumulation of nutrients in the biomass and restoring the soil's physical and chemical properties (Brown and Lugo, 1992). The uncertainties in biomass accumulation rate in this type of ecosystem limit the understanding of the true role of tropical forests as sources or sinks of atmospheric carbon (Kauffman et al., 2009). One of the major barriers to the development of realistic simulations is the lack of detailed information on biophysical parameters such as canopy cover, growth rates, and stem and root biomass (Asner et al., 2003).

Leaf area index (LAI) is an important parameter for studies of vegetation structure, since it is associated with physical processes such as evapotranspiration, carbon dioxide flows, light interception, throughfall and stemflow (McWilliam et al., 1993). The indirect determination of LAI by measuring the radiation that pass through the canopy is an important tool for monitoring the ecosystem's primary productivity (Asner, 1998; Arias et al., 2007).

LAI in Amazon forests ranged from 4.79 ± 1.27 (m^2 of leaf per m^2 of soil; mean ± standard error) to 4.96 ± 1.30 using hemispherical photography in the Biological Reserve of Jarú (Caruzzo and Rocha, 2000), 4.63 in Ji-Parana, 6.10 in Manaus, and 5.38 in Marabá through the analysis of litter (Roberts et al., 1996). Malhado et al. (2009), using LAI-2000, found 5.07 in the Tapajos National Forest. However, there are no published studies which report the seasonal LAI variation during the year in the Amazon region, particularly in areas of secondary vegetation.

In addition to above-ground biomass, substantial primary production occurs below the soil surface in the root system (Nepstad et al., 1994), and this plays an important role in the carbon cycle (Vogt et al., 1996) nutrient and water uptake but can also shape plant communities by hydraulic lift (Maeght et al., 2013). The root production varies with soil and vegetation types (Jackson et al., 1997). The roots are the major source of soil organic carbon, and plants depend on them to take up minerals and water, to support canopy physiology, and to store carbohydrates (Dornbush et al., 2002; Matamala et al., 2003). Thus, the measurement of root biomass and root growth becomes an important tool for understanding the biogeochemical processes in the ecosystem (Silver et al., 2005). However, this type of measure is particularly difficult because the root extraction is time-consuming and requires intensive field and laboratory work, which disturbs the site being studied.

Tropical soils may be important carbon sinks when well managed (Lugo and Brown, 1993), however, it is assumed that after the conversion of the area for agricultural use, the soil is depleted in carbon, and there may be a recovery in the organic carbon concentration during the fallow period (Raich, 1983; Cerri et al., 1991; Lugo and Brown, 1993). The roots are the largest carbon pool and source within the soil profile, and they are a major contributor to soil respiration (Gill et al., 2002). Consequently, the root dynamics are an important mechanism for carbon and nutrient cycling between plants and soil (Dornbush et al., 2002; Poszwa et al., 2002).

Information about the production of fine roots and aspects that may influence the root dynamics in secondary tropical vegetation is essential in order to understand the role of these ecosystems and to predict how changes caused by deforestation can modify the ecological structure of the ecosystem (Vogt et al., 1993). Studies show that the highest soil carbon concentration is near the surface, up to 200 cm in depth. However, Nepstad et al. (1994), Trumbore et al. (1995) and Jipp et al. (1998) emphasized the importance of root penetration in deep layers of soil for water supply to plants during dry seasons, and this carbon in the root system is an important carbon sinks in the Amazon. In the northern state of Pará, soil carbon storage in areas traditionally used for slash-and-burn agriculture, in a soil profile to 6 meters, did not differ significantly between primary forest (196 Mg C ha^{-1}) and secondary vegetation (185 Mg C ha^{-1}) (Sommer et al., 2000).

Efforts are needed to increase confidence in carbon accounting among different land uses, especially in tropical forest ecosystems that often need to turn to default values, given the lack of precise and reliable site-specific data to quantify their carbon sequestration.

The first objective of this study was to gain insight into the seasonal variations in LAI and root biomass in secondary forests of different ages. The hypothesis was that seasonality decreases with the age of secondary forests because roots penetrate deeper into the soil, alleviating water stress and allowing plants to maintain high LAI values longer during the dry season.

2. Materials and methods

This study took place in an experimental area of EMBRAPA-Amazonia Oriental, in Igarapé-Açú city (1°07′44″S and 47°37′12″W), in the state of Pará (Brazil), where most of the municipal areas are occupied by small farms. The region is characterized by slash-and-burn systems, where secondary vegetation of different ages coexists next to agricultural crops and grasslands. During the fallow period, secondary vegetation regenerates as fallow vegetation from roots and stumps that survived the cropping period.

The rainfall ranged from 1700 to 2400 mm year^{-1} (Sommer et al., 2000), with a dry season during July-December (346 mm on average during this period). The remainder of rainfall is distributed from January to June. Average annual temperature is between 25 and 26 °C (Sommer et al., 2000). In this study, the rain was collected monthly in an automatic station located at 2.0 km from the experimental area.

The study area has a flat topography and Rego et al. (1993) classified the dominant soils in the region as Dystrophic Yellow Latosol Stony Phase I in the Brazilian Classification, corresponding to Sombriustox in US Soil Taxonomy. Soil texture was sandy loam at the surface and sandy-clay in deeper layers (Thielen-Klinge, 1997; Sommer et al., 2000). These soils are characterized by being extremely sandy and having a low nutrient content, low cation-exchange capacity (CEC), and high aluminum (Al) concentration in a profile of 600 cm depth (Table 1).

The plant diversity in the secondary vegetation in the same region is quite high, reaching a total of 827 species, of which 508 species are woody (Baar et al., 2004). In the same study area, Denich (1989) studied secondary vegetation (area of 250 m^2) with an age of 1 to 10 years, and among individuals ≥30 cm in height, he

Table 1
Average distribution of the chemical properties and texture of the soils of the study region (n = 7), adapted from Thielen-Klinge (1997) and Sommer et al. (2000).

Analysis	Soil layers (cm)				
	0–5	50–100	150–200	350–400	550–600
$pH_{(H2O)}$	5.4–5.8	5.0	4.8	4.8	5.2
N_{Total} (mg g^{-1})	0.7–1.2	0.6	0.6	<0.1	<0.1
$P_{(Mehlich\ I)}$ (mg kg^{-1})	2.5–5.0	1.0–2.0	<1.0	<1.0	<1.0
$Al_{(exchangeable)}$ (cmol + kg^{-1})	0–0.6	0.81	0.41	0.26	0.13
$CEC_e^{(1)}$ (cmol + kg^{-1})	1.6–4.1	1.14	0.73	0.44	0.26
Sand (%)	80.0	65.0	65.0	68.0	72.0
Silt (%)	10.0	8.0	10.0	8.0	8.3
Clay (%)	11.0	27.0	25.0	24.0	22.0
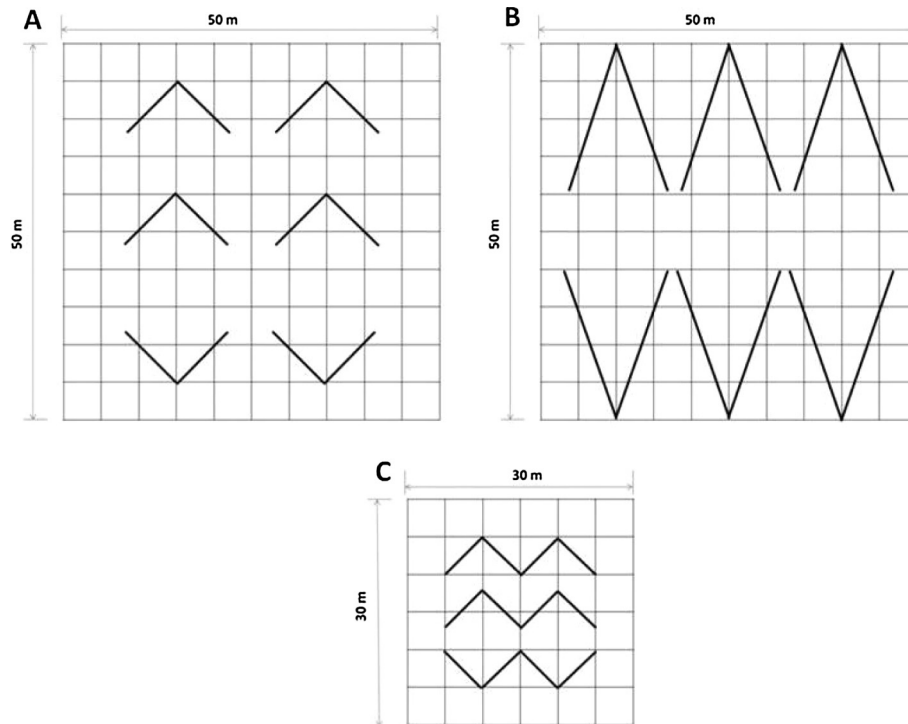
Fig. 1. Schematic diagram of the study plots, with the points used for the measurements. The letters A (n = 3), B (n = 3) and C (n = 3) represent the secondary vegetation in stage 6 (90° optical aperture), stage 10 (45° optical aperture) and stage 1 (90° optical aperture), respectively. The optical aperture represents the amount of light that came in the LAI-2000 instrument as explained in the Material and Methods.

found 36 families (81 species), with the most common being Myrtaceae and Fabaceae. According to studies conducted in the Brangantina region (with 8,710,774 km^2), the floristic composition of the fallow was very similar (Baar et al., 2004; Clausing, 1994; Denich, 1989; Nunez, 1995; Vieira, 1996). Ninety-five percent of the recorded species have been replicated and non-common species are rare (Baar et al., 2004).

2.1. Leaf area index (LAI)

For this study, different areas of secondary vegetation were used, with three distinct ages (1, 6 and 10 years old), which will be referred to as stage 1, 6, and 10, respectively. The age corresponded to the time since abandonment of the areas after two years of cultivation (age class). In each age class, three 50 × 50 m plots were demarcated (Fig. 1A–C). Indirect and direct measurements for LAI were combined to provide robust estimates. Indirect methods for LAI study, which measure the penetration of light passing through the canopy by optical instruments, have been commonly used for comparisons between different canopy architectures (Welles and Norman, 1991). These approaches need to

be employed with caution due to the significant errors that may occur (McWilliam et al., 1993). Combining direct and indirect methods can provide a robust estimate of the canopy structure and give useful insights into the aboveground biomass (AGB) in different ecosystems when laborious direct measurements are used to calibrate the easier light-penetration measurements.

First, an indirect method was used for LAI measurement, with a LI-COR LAI2000 – LI-COR Plant Canopy Analyzer (PCA); calibration of this machine to produce an appropriate LAI was done, with the procedure described in detail by Welles and Norman (1991). The PCA uses an optical sensor and measures diffuse radiation (wavelengths between 320 and 490 nm) at five angles: from 0.0 to 12.3°, 16.7 to 28.6°, 32.4 to 43.4°, 47.3 to 58.1°, and 62.3 to 74.1°. This effectively divides the canopy into five layers, and light attenuation by these layers is proportional to the area of leaves that intercepts the light. However, not all the attenuation is due to leaf area; some is due to trunks, branches, vines, etc., and this can lead to overestimation of LAI.

The experiment was conducted on three small farms, and in each farm, the three different age classes were delimited. The LAI was obtained using two sensors: a reference sensor that measured

the amount of light in an open area (full sun), and a second apparatus used for sampling within the plots. Measurements in open light and under the canopy were made simultaneously, and the difference in light interception was attributed to leaf area. Measurements were conducted monthly for one year, when the sun angle was below 30°.

To decrease the influence of surrounding vegetation on the plot, a 300 cm firebreak was maintained without vegetation around each plot for the duration of the experiment. Predetermined points for monthly LAI measurements were marked with pickets in each plot. In the stage 1 plots, the PCA's sensor was placed at the soil level and in the other stages, in order to avoid interfering of the herbaceous plants, the sensor was placed at a height of approximately 0.8-m. Measurements were made with an openness reducer on the optical sensor, with an opening of 45° to secondary vegetation in stage 10 (Fig. 1B) and 90° in the other two treatments (Fig. 1A and C). The restriction of the opening optic angle was used to reduce the influence of spatial variation in the canopy structure, especially in natural ecosystems (Welles and Norman, 1991).

2.2. LAI calibration

The LAI calibration was done during the dry season (August to September) using six subplots of 2.0 m^2, within one of the three plots in stage 6 mentioned above. This stage was used because in the secondary forest the maximum increment in the basal area is in the 6th year (Neeff and Santos, 2005). Six areas were demarcated with a 90° angle, forming a triangle (200 cm on each side and a 280-cm hypotenuse), with the apex directed to the measuring point as Fig. 1A shows. Before the first LAI reading all leaves between 0.0 and 10.0 cm above ground level were removed and weighed on a field balance with a precision of 0.01 kg. Three sub-samples were collected, weighed with a precision balance (0.001 kg), and transported in plastic bags to the laboratory for analysis of leaf area and dry weight.

After removing the leaves below 10 cm above ground level, the first LAI reading was made, and all leaves between the heights of 10 and 80 cm were collected, weighed, and subsampled as above. The process was repeated for layers at the following heights: 80–130 cm, 130–200 cm, 200–300 cm, 300–400 cm, and 400–600 cm.

In the laboratory, the green samples were placed in an area meter (LI-COR 3200), which consists of a plastic mat and a video camera attached to a computer. All leaves from each sample were placed separately on the mat and cumulative leaf area was determined by LI-COR 3200 Area Meter. After repeating the leaf area measurement for each sample three times, leaves were dried in an oven at 70 °C until at a constant weight. All samples were then weighed on a precision balance (precise to 0.0001 kg). From that, the correlation between dry weight and leaf area was applied to all biomass measurements to estimate the leaf area of each canopy layer sampled. This calibration was applied to all measurements over the 12 months of sampling. Accumulation leaf biomass was calculated by the subtraction of the biomass found in the current month and the previous month, with the addition of accumulated of the previous month.

2.3. Root growth rate (RGR)

Root growth was studied using the ingrowth bag method (Vogt et al., 1996; Campbell et al., 2002). In each LAI monitoring plot, six points were marked, with 10.0 m between points and 4.0 m from the border of a 10-year secondary forest, (3.0 m distance from the 6- and 1-year secondary forest borders). At each point, three holes were made, each with an auger (16 cm internal diameter) to a depth of 4.0 m. The three holes were arranged in a triangular shape, 0.5 m apart from each other. Thus, there are fifty-four semi-annual sampling points for RGR in each studied secondary-forest age.

The ingrowth bags, made with 2.0-mm nylon mesh and with an average area of 50.3 cm^2, were made with heat presses. The bags were filled with moist subsoil (400-cm deep) that had been sieved in 2.0-mm mesh to remove all organic material above 2.0 mm in diameter, and weighed. The first bags were placed at the beginning of the dry season, and each bag was tied to a nylon string (5.0 mm diameter) previously cut to the length of the depth at which the bag would be placed in the hole. After placing each bag, the hole was backfilled with soil to the depth of the following bag, and so on until the hole was completely filled. The depths were 0, 30, 50, 100, 200, 300, and 400 cm.

After six months, the bags were removed with the aid of the same auger used previously. The soil was removed from each hole to the height at which the ingrowth bag was placed, and with the aid of the nylon string, each growth bag was pulled up, placed in labeled plastic bags, and taken to the laboratory. In the laboratory, all bags were first cleaned of roots growing out of the bag with the aid of shears, dried at 70 °C for 72 h, weighed to calculate the soil bulk density in the ingrowth bag, and then washed in running water with a 2.0-mm sieve. As a result of the short time in the soil, any roots found growing inside the ingrowth bags were alive. The roots inside the bag were collected, dried in an oven at 70 °C, and after the weight stabilized, the dry mass was determined. All root samples were kept dry in plastic bags until they were weighed.

In order to compare the different samples, and because there was no control on the density of the soil inside the ingrowth bag, although each ingrowth bag was the same size, a root growth rate (RGR) method was used to correct RGR data for soil mass. The RGR_{td} was determined for each sample by the relationship between the weight of the roots that grew (root increment) in the bag (RG_{td}, mg), at a specified time interval (t), at a definite depth (d), multiplied by the soil density in the bag (D_{td}, g cm^{-3}). This correction was made because the soil densities inside the ingrowth bags were not identical, ranging from 1.238 to 1.630 g soil cm^{-3}, and there is an inverse relationship between the soil density and root development (Bauhus and Messier, 1999; Campbell et al., 2002).

$$RGR_{td} = RG_{td} * D_{td}$$

At the same time that the ingrowth bags were removed, new ingrowth bags were placed in the same holes using the methodology described above, and then removed after 6 months.

2.4. Statistical analysis

ANOVAs were used to test the effects on seasonal variation of LAI and RGR within each area, as well as between different ages of secondary vegetation and in the soil depths. Two-way analyses of variance with repeated measures were used to test the effects of soil depth, collection period, and interactions of soil depth and collection on fine-root mass. After identifying the differences between the areas, Tukey's HSD test (P < 0.05) was used to measure their significance. The statistical analysis was performed using "Systat Software" (STSC, Rockville, MD, U.S.A.).

3. Results

During the year under study, rainfall was 1968 mm, and in the dry season (July to December), rainfall was only 357 mm, with November the driest month (Fig. 2). The remaining 1621 mm was distributed throughout the rainy season, with the highest rainfall in March.
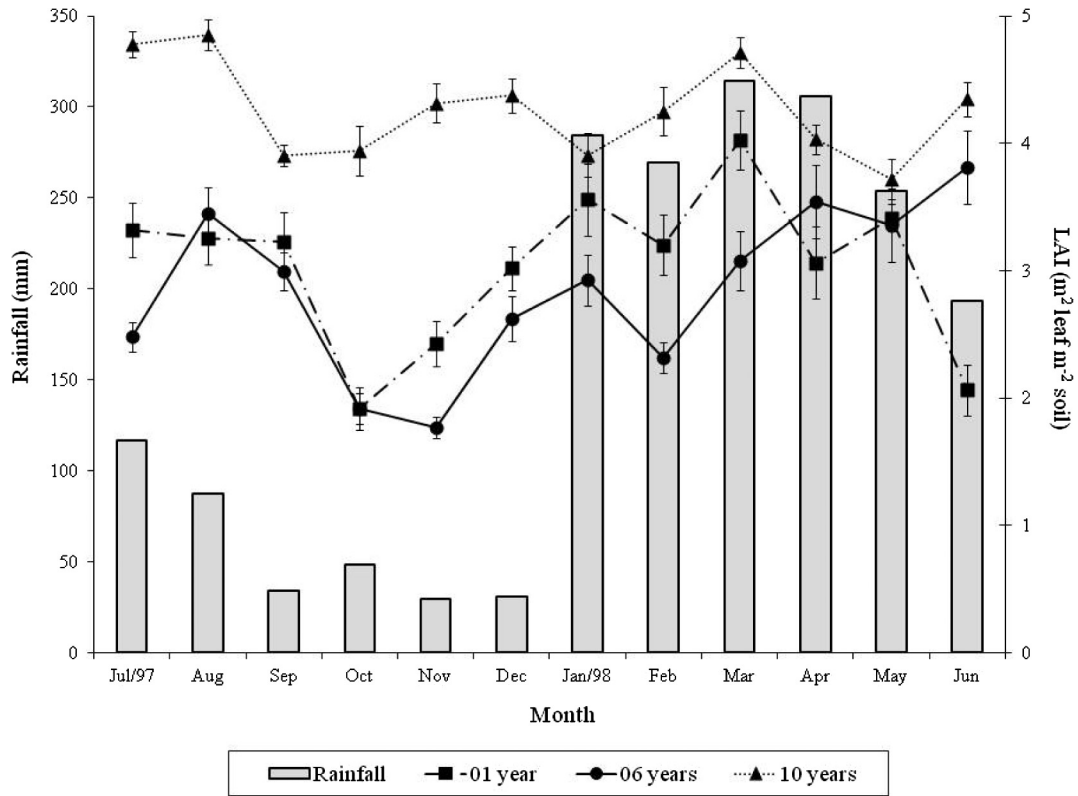
Fig. 2. Monthly leaf area index (LAI) at different ages of secondary vegetation (lines) related to rainfall (bars) during one year of sampling. The points represent mean values (n = 18) and the bars represent standard error of the mean.
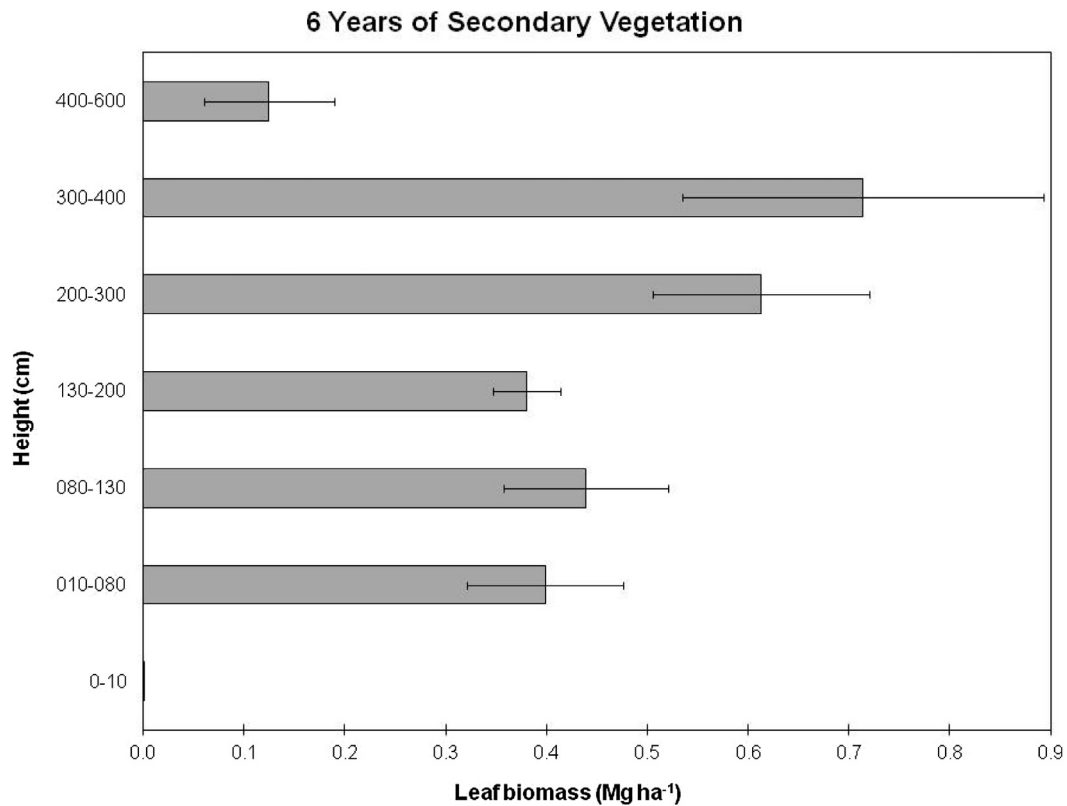

Fig. 3. Leaf biomass (Mg ha^{-1}) at different canopy heights (cm) for secondary vegetation in stage 6. The bars represent standard error of the mean (n = 6).

3.1. Leaf area index (LAI)

The maximum LAI values found during the study were 5.80, 5.18, and 5.89, with averages of 3.07 ± 0.07 (mean ± SE), 2.89 ± 0.07, and 4.28 ± 0.05 for the secondary vegetation of 1 (n = 199), 6 (n = 200) and 10 years (n = 205), respectively. When comparing the annual average of LAI, there were significant differences (p < 0.01) between treatments, and the post hoc separation analysis showed that the LAI of the secondary vegetation in stage 10 was higher than the LAI of the other two treatments. Additionally, the secondary vegetation in stage 1 has a higher mean LAI (p < 0.05) compared with stage 6.

Comparing the seasonal periods, the secondary vegetation in the dry season showed a mean LAI of 2.86 ± 0.09, 2.61 ± 0.08, and 4.40 ± 0.06, and in the rainy season, the LAI was 3.31 ± 0.11, 3.21 ± 0.11, and 4.17 ± 0.07 for sites with secondary vegetation in stage 1, 6, and 10, respectively. The two younger ages showed a significant LAI decrease (p < 0.01) in response to the drastic rain reduction at the beginning of the dry season (Fig. 2). Between stage 1 and 6 a significant difference was found (p < 0.05), and this difference was higher compared with secondary vegetation in stage 10 (p < 0.01) in both seasons, which was stronger during the dry season (Fig. 2).

There was significant (p < 0.01) monthly and seasonal variation in canopy cover between stages 1 and 6, which was less strong among older secondary vegetation (Fig. 2). During the dry season, the LAI of the secondary vegetation in stages 1 and 6 decreased to 1.40 and 1.53, respectively. But in the secondary vegetation in stage 10, there was only a small decrease of 0.95 in LAI during the same period. In the secondary vegetation in stage 1 and 6, there was a LAI increase of 1.62 ± 0.25 and 1.14 ± 0.33, respectively, between the middle of the dry season (October) and the beginning of the rainy season (January).

3.2. Calibration of the leaf area index (LAI)

In stage 6 the average biomass of leaves was 2.67 ± 0.35 Mg ha^{-1}, with a significant difference between the canopy layers. The highest biomass was found in layers 300–400 and 200–300 cm above ground (Fig. 3). There is an important stratification inside the canopy, and the highest leaf biomass is in direct contact with sunlight, with 54.4% of leaves above 200 cm. It is also important to note a significant leaf biomass below the height of 130 cm, which corresponds to 31.4% of the total leaf biomass.

Regarding the light interception by leaves, four foliage layers can be identified in these stands: 0–10 cm, 10–200 cm, 200–400 cm and 400 to 600 cm (Fig. 3). However, the LAI-2000 data underestimates the leaf area in 26.9% (Table 2), especially where the layers were more biomass-rich (200–300 and 300–400 cm).

3.3. Root growth rate (RGR) and root increment

Root growth rate at different ages (Fig. 4) showed significant differences (p < 0.05) at most depths in the same seasonal period

of the year. In the dry season period, RGR was higher (p < 0.05) in the upper soil layers (0–30 cm), especially for the 10-year-old plots in the dry season (Fig. 4C). All ages showed a decrease in the RGR with depth in the profile, up to 200 cm depth in both seasons (Fig. 4).

The RGR when compared with the root increment (fine-root biomass in the ingrowth bags), showed statistically significant differences (p < 0.01) in the two seasons. This is due to the fact that we only consider biomass of the roots inside the ingrowth bag, and do not consider the soil density in these bags; because of this, the results could be overestimated. However, for comparison with other published studies, root increment was used.

The present study revealed that the fine-root increment was 581.2, 699.7 and 718.0 kg ha^{-1} yr^{-1} for stages 1, 6, and 10, respectively (Table 3). Root increment throughout the soil profile during the year showed no statistical difference between the total biomass increases of fine roots in different age plots and between the seasons (Table 3). However, fine-root increment showed a significant difference (p < 0.05) between depths and for the seasons at each age of secondary vegetation (Table 3).

Comparing the soil profile from 0 to 50-cm with deeper soil during the dry season showed that the younger and older secondary forests had greater root increment on the surface (Table 3), that is, 61.50% and 59.00% of the root increment increase was in the upper 50-cm of the soil for the plots in stage 1 and 10, respectively. However, at the site of secondary vegetation in stage 6, there was no difference (p > 0.05) between the two soil profiles mentioned above (Table 3).

In the rainy season, the secondary vegetation in stage 6 showed a significantly higher root increment (63.5%) in the layers below 0.5-m, whereas the other age classes did not show a large difference between the two profiles. This resulted in 52.9% and 47.0% of the fine-root increment below 50-cm of soil profile for secondary vegetation in stage 10 and 1, respectively (Table 3). In the majority of analyzed depths, a lower root growth was observed in the rainy season compared to the dry season (Fig. 4).

4. Discussion

4.1. Leaf area index (LAI)

This study demonstrated that LAI varies with season and this variation was smaller in the 10-year-old secondary vegetation compared to the younger secondary forests. The secondary vegetation variation between 1 and 6 years seems to be related to the use of the pre-established root system from before the cutting of vegetation for agricultural use. As the secondary vegetation regrows and biomass accumulates (six years of secondary vegetation), the growth of the root system still does not supply enough water to meet the demands of canopy transpiration, and drought stress produces a severe reduction in LAI.

The LAI averages presented in this work are lower than the LAI of 4.90 for an average of 61 observations in tropical forests in Brazil

Table 2
Canopy height (cm) with corresponding measurements of total leaf weight (g m^{-2}), total leaf area (m^2 m^{-2}) and LAI measured by LAI 2000 (LiCor), in the secondary vegetation in stage 6, measured in the dry season. Standard errors in parentheses (n = 6).

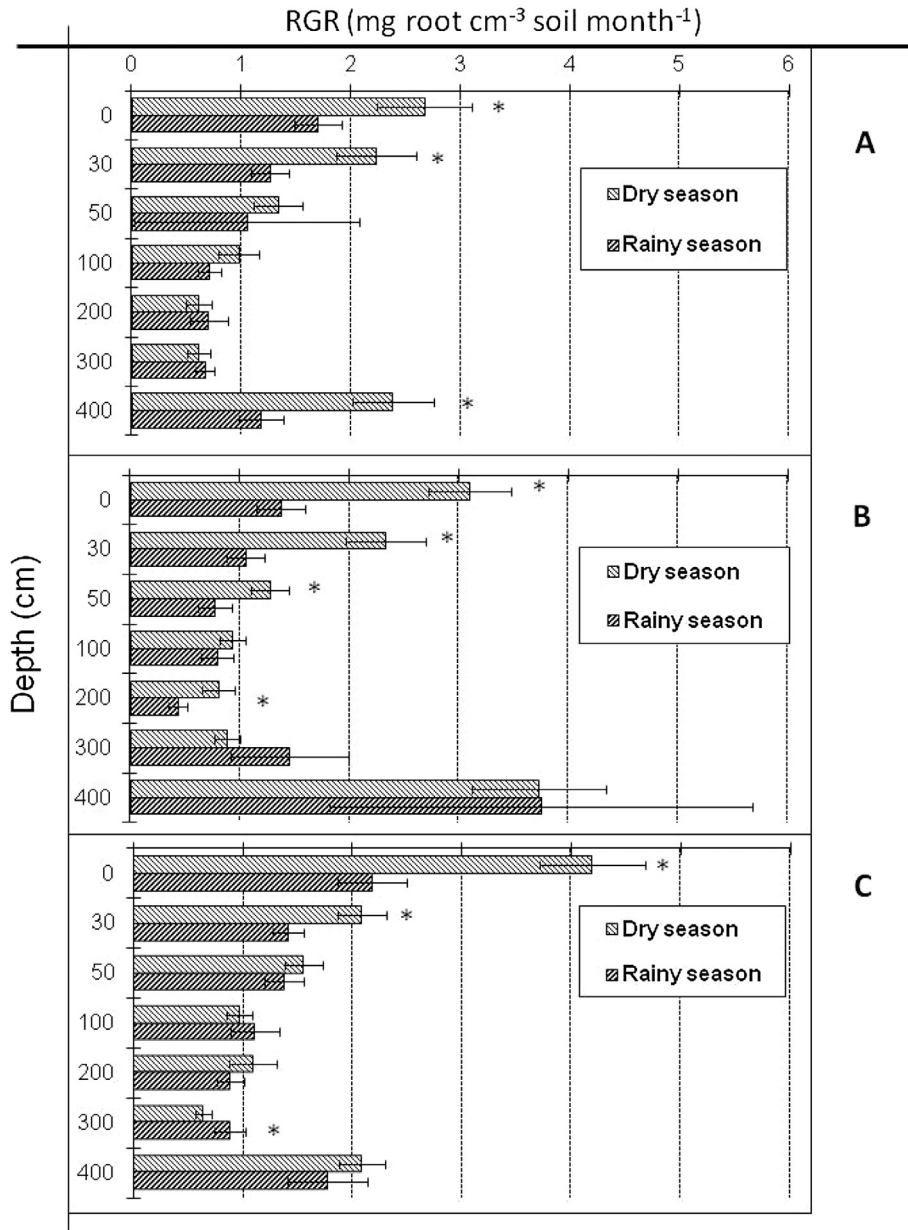| Canopy height (cm)	Dry weight of leaves (g m^{-2})	Total leaf area (m^2 m^{-2}) (A)	Measured LAI (m^2 m^{-2}) (B)	(A–B) (m^2 m^{-2})
0–10	0.03(0.00)	0.001(0.00)	NM	
10–80	39.86(0.78)	0.02(0.00)	0.05(0.01)	−0.03
80–130	43.89(0.82)	0.71(0.11)	0.51(0.10)	0.20
130–200	38.03 (0.33)	0.55(0.05)	0.63(0.17)	−0.08
200–300	61.30(0.08)	1.07(0.19)	0.82(0.24)	0.25
300–400	71.40(1.79)	2.71(1.18)	0.82(0.23)	1.89
400–600	12.49(0.65)	0.40(0.11)	0.45(0.14)	−0.05
0–600	266.97(35.04)	5.24(1.24)	3.83(0.64)	1.41

Fig. 4. Root growth rate (RGR, box) for secondary vegetation in stages 1, 6, and 10 (A, B and C, respectively) at different depths for the two seasons. The asterisks and bars represent significant differences (p < 0.05) and standard error of the mean (n = 54), respectively.

Table 3
Mean root increment (kg root ha^{-1} yr^{-1}) at different depths (cm) for three secondary vegetation ages (n = 54; standard error in parentheses) sampled during the dry and wet season in Igarapé-Açú (PA). The lower case letters represent the comparison between the depths in the same season and age, and capital letters compare the seasons in the same age and depth.

Depth (cm)	Stage 1		Stage 6		Stage 10	
	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season
0	74.4(10.5)[aA]	64.9(8.6)[aA]	83.9(10.0)[aA]	52.4(8.3)[bB]	115.6(10.8)[aA]	71.4(6.4)[abB]
30	61.4(8.5)[abA]	42.7(5.4)[bA]	63.8(9.7)[abA]	37.0(5.4)[cB]	56.4(5.6)[bA]	49.6(3.9)[bA]
50	38.6(5.8)[bcA]	36.3(5.7)[bA]	35.8(4.7)[bA]	30.9(6.2)[cA]	43.8(4.7)[bcA]	45.0(3.9)[bA]
100	26.9(4.5)[cA]	27.0(3.8)[bA]	26.6(3.4)[bA]	28.7(4.6)[cA]	29.1(3.1)[cA]	38.4(4.8)[bA]
200	18.6(3.9)[cB]	28.3(6.7)[bA]	24.7(4.8)[bA]	17.8(2.7)[cA]	34.3(6.9)[cA]	37.5(4.4)[bA]
300	18.4(2.9)[cB]	26.9(3.4)[bA]	26.8(3.9)[bB]	48.4(12.2)[bA]	21.8(2.4)[cB]	35.1(3.9)[bA]
400	71.5(8.9)[aA]	45.3(7.4)[abA]	108.4(17.0)[aA]	114.5(38.8)[aA]	65.0(6.2)[bA]	75.2(14.7)[aA]
Total	309.9	271.3	370.1	329.6	365.9	352.0

(Asner et al., 2003). However, the annual average and seasonal amplitude for the secondary vegetation in stage 10 was similar to the results Juárez et al. (2009) obtained in a logged forest near the Tapajos River. Selaya et al. (2008) studied secondary forests in Bolivia, which were in early stages of succession, and found LAI values of 1.66 and 3.54 for secondary vegetation between 0.5 and 2.0 years of age, respectively, which does not appear to be different from the results presented in this work, and is very similar to the secondary vegetation in stage 1. Related to the results presented here, Vieira et al. (2003), studying secondary vegetation in the same region, found a higher LAI in 3 and 6-year-old plots during the rainy season, while 10-year-old stands had constant LAI during the year. The secondary vegetation of stage 1 had a higher mean LAI when compared to stage 6. This difference could be related to a lower ratio between the volume of wood and leaves, or a larger number of individuals per m-2, which has been observed in younger secondary forests (Coelho et al., 2003).

The leaf area increase in the early secondary vegetation during the dry season seems to reflect the need to increase plant uptake of available solar energy in this season, as Myneni et al. (2007) suggested. These same authors showed that the LAI was positively correlated with solar radiation and negatively correlated with precipitation, i.e., one can expect an LAI increase in the dry season and an LAI reduction in the wet season. With that, the results presented here indicate that leaf production is probably related to physiological factors (photosynthesis and transpiration), which seem to continue to benefit from root systems established before the slash and burn of secondary vegetation for agricultural production. The LAI estimated by the micrometeorological data was higher in the wet and dry–wet seasons due to an increase in forest vegetation growth as a consequence of increased water availability (Pinto-Júnior et al., 2011). On the other hand, Vasconcelos et al. (2012) found that the increase in aboveground net primary productivity occurred in response to the dry season of the previous year and suggest that the regrowth of the rainforest may be sensitive to the seasonality of the rains.

However, secondary forests of 1 and 6 years old react significantly with the rainfall decrease, reducing the LAI, with perceptible intensity in stage 6 (Fig. 2). Denich (1989) found that all the individuals above 50 cm tall derived from sprouts, and these data show that slash and burn of secondary vegetation for agricultural production seems not to have produced significant root death during stress periods, which means that deep water absorption is not hindered. With these deep roots from previous rotations, the canopy water supply can be restored when stems regenerate. From secondary vegetation in stage 10, the root system supplies adequate water for tree development, as there is no decline in leaf area during the year (Fig. 2). In the same way shown by Asseng et al. (1998), the data show that the evapotranspiration declined under water deficit due to a decrease of leaf area, but probably the water uptake in deeper layers increases by increased root biomass.

4.2. Leaves and roots biomass

The LAI dynamics are a key parameter for forest modeling studies and to determine the vegetation role in the carbon cycle (Clark et al., 2008) and have a potentially strong effect on biomass productivity (Lohbeck and Martínez-Ramos, 2015). Therefore, it is very important for biomass model development and parameterization to include direct measurements of leaf area (MacFarlane et al., 2007). The results showed in this work suggest that after 10 years the secondary regeneration maintains a stable leaf area. However, the monthly and seasonal LAI variations produced by the 10 year-old secondary vegetation had amplitude approximately twice as large as the variation found by Malhado et al. (2009) when studying a primary forest in the FLONA of Tapajós.

The leaf biomass measured in this study was higher than that presented by Hughes et al. (2000) studying a site with 4 years of secondary vegetation in Marabá (PA), using a methodology of correlation between wood and leaves, and half of that found by Chave et al. (2008) studying a primary forest in French Guiana. Contrary to the results of Asner et al. (2003) and Malhado et al. (2009), the data showed that the LAI-2000 underestimates the total leaf area by approximately 26.91% (Table 2), which is in agreement with the results presented by Olivas et al. (2013) in a primary rainforest where LAI-2000 underestimated the leaf area by 17.70%.

It is important to note that at some heights the difference between leaf biomass is minimal, with the largest error at the height with the largest leaf biomass (Table 2). Field observations showed that the clustering, overlapping, and non-randomness of leaves seem to be the largest sources of error when measuring LAI by indirect methods (Liu et al., 2015).

In the present study, the leaves reach a total of 2.70 Mg ha^{-1}, which does not differ from data presented by Kenzo et al. (2010) in the initial decade after shifting cultivation in Malaysia, and a little lower than that presented by Feldpausch et al. (2004) of 3.48 Mg ha^{-1}, in a secondary forest of 4–6 years following abandonment of a pasture in central Amazonia. Although biomass allocation to the leaf component was limited to only 1.3–2.8% in primary tropical rainforests (Jordan and Uhl, 1978), tropical secondary forests have shown a relatively large biomass allocation to the leaf component at early stages of succession, ranging from 2.0% to 15.0% (Uhl and Jordan, 1984; Andriesse and Schelhaas, 1987; Lugo, 1992; Feldpausch et al., 2004). This larger allocation to leaf biomass is considered to be one of the causes of higher productivity at the early stage in tropical secondary forests compared with the old secondary and primary forests (Kenzo et al., 2010).

When sites under slash and burn are quickly abandoned after a short cultivation period, estimated values of LAI reach the levels of mature forest in 5 years (Jordan and Uhl, 1978; McWilliam et al., 1993). However, when sites under slash-and-burn agriculture are subjected to longer crop cycles, the LAI recovery may require more time to return to the values found in a mature forest (Vieira et al., 2003). The secondary vegetation in this region of the study has been managed through slash and burn for more than 100 years and the number of forest fires adversely affects biomass recovery (Wandelli and Fearnside, 2015), therefore, we would expect a much lower leaf area than presented in this study, although the LAI found in this study agrees with the literature.

The total root increment for different ages of secondary vegetation can be found in Sommer et al. (2000) because their study was performed at the same study site. Importantly, all roots that grew in the ingrowth bags were found to be alive. The secondary vegetation in this region captures approximately the same amount of carbon in the root system during the year, regardless of age or succession stage. The high fine-root increase in the secondary forests is comparable to the total growth of roots in old forests where the thick root growth and storage of carbon in larger roots are higher than in fine roots (Nepstad et al., 1994; Addo-Danso et al., 2016). The results presented here are similar to those showed by Lima et al. (2012), who studied a secondary forest of 10 years of age and compared only the first 10-cm depth, and greater than the roots increment presented by Fonseca et al. (2011), and only 20.5% of the root increment of a tropical forest (Addo-Danso et al., 2016). Another important point is that the root growth, when examined up to 10-cm depth (Table 3), seems independent of seasonality, which differs from the results presented by Lima et al. (2012).

This study appears to corroborate the work of Sommer et al. (2003) and Nepstad et al. (1994) with reference to the importance of deep roots in maintaining an evergreen canopy in the secondary forest. However, the present results do not agree with Sommer

et al. (2003) about the relative importance of roots below 100 cm depth, and indicate a greater importance of these roots, especially those that grow below 400 cm to supply water that maintains evapotranspiration (Maeght et al., 2013; Lindh et al., 2014; Callesen et al., 2016). As Comte et al. (2012) showed in their work, it is also necessary to take into account that the deepening of the root system may not be related to the search for nutrients, because the deeper horizons are extremely nutrient poor (Table 1), given the fact that this region has been managed using a system of slash and burn of secondary vegetation for over 100 years (Denich, 1989). On the other hand, deep root exudates may promote chemical wear of soil mineral components (Maeght et al., 2013; Callesen et al., 2016).

Accurate estimation of biomass changes in tropical secondary forests will contribute to better calculation of forest carbon storage in the region. Uncertainties in the rate of biomass accumulation in these forests are an important gap in our understanding of the role of tropical forests as sources and sinks of atmospheric carbon (Kauffman et al., 2009; Rozendaal and Chazdon, 2015), particularly for belowground components (Brown and Lugo, 1992). In the same way that Schedlbauer and Kavanagh (2008) showed, there is no significant difference in root increment between the different ages and the seasons. This is important information for carbon sequestration models in relation to land-use changes and the development of secondary vegetation. The greater root biomass seems to concentrate in the top centimeters of soil (Nepstad et al., 1994). However, in agreement with Davidson and Trumbore (1995) and Trumbore et al. (2006), deeper roots should be taken into account in climate-change models in relation to soil carbon storage and water flows in the soil-plant-atmosphere system. Similarly to Saleska et al. (2007), high root growth at depth is responsible for the maintenance of an evergreen canopy in Amazonian secondary forests despite a 5- to 6-month dry season or El Niño events, which justifies no decrease in LAI during seasonal periods in secondary forests with over 10 years of age.

Secondary forests in the Bragantina region were accruing biomass more rapidly in 10-year-old secondary forests (5.5 Mg ha^{-1} yr^{-1}) than in the 20–40-year-old ones (3.3 Mg ha^{-1} yr^{-1}) (Johnson et al., 2001). During 4 and 6–10 years of succession, vegetation in the Bragantina region exhibits an average tree basal area of 2.7 and 3.83 m^2 ha^{-1}, respectively (Tucker et al., 1998). In secondary forests of 5, 10, and 20 years, Salomão et al. (1998), using allometric equations, found 13.0, 44.0, and 82.0 Mg ha^{-1} of AGB, respectively, with an average annual increment of 4.0 Mg ha^{-1}, which implies a removal of 2.0 Mg C ha^{-1} year^{-1} from the atmosphere through photosynthesis. These results do not differ significantly from the biomass accumulation presented in this work.

After several decades of tropical studies of secondary vegetation regeneration, we still lack the ability to make strong predictions about carbon storage and successional shifts in forest development and regeneration times for abandoned sites to attain primary-forest equivalent biomass. Aboveground carbon accrual is rapid (Rozendaal and Chazdon, 2015), but below-ground gains represent the largest potential area for continued accumulation and management. Population increase, land tenure programs, and agricultural policies are the main driver of the increase in shifting cultivation in the Amazon region (van Vliet et al., 2013). This increase may lead to a further intensification of land use, changing the regeneration dynamics, reducing the fallow years, and preventing the reestablishment of secondary forests.

5. Conclusions

In conclusion, LAI is a promising, simple to measure (optically) ecological index for monitoring the impact of silvicultural treatment and the effect of site physical characteristics on stand growth. The error produced by the use of optical equipment is underestimated in the 6-year-old secondary vegetation. This error should be taken into consideration when LAI values are used to model the effects of land-use change on carbon stock, carbon fluxes, and evapotranspiration in the soil-plant-atmosphere system. These results also argue for systematic calibration of LAI measurements based on light diffusion.

The roots are growing evenly in the different secondary vegetation stages due to stem retention and maintenance of its root system to search for nutrients and deep water. There is root-growth seasonality with more intensification in the dry season, regardless of secondary-vegetation age. These studies clearly indicate that deep root into secondary forests areas is essential to increase our understanding of ecosystem ecophysiology, but also of community ecology and geochemical cycles.

The results indicate a need for caution when using foliage biomass or LAI estimates calculated using different models, especially if the estimates are to be used as an input for other models. The information presented here is important for understanding the contribution of the sites covered with secondary vegetation in carbon cycling and water supply, mainly because these ecosystems are expanding in site coverage as primary forests areas decrease. Therefore, it is very important for parameterization and development of models that require direct measurements to predict the true contribution of these ecosystems to biogeochemical cycles in the future. With the data presented in this study, we can reduce the uncertainties in the rate of biomass change with the secondary-vegetation growth and in selecting an appropriate model, particularly for belowground components, improve the accuracy of atmosphere carbon flux estimates in tropical sites.

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