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ORIGINAL ARTICLE

Biomass of fine roots in different land cover types at the 'arc of deforestation', Brazil

Biomassa de raízes finas em diferentes tipos de cobertura do solo no 'arco do desmatamento', Brasil

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RESUMO: This study aims to evaluate the effect of land cover type, soil properties, and vegetation structure on fine root biomass, and examined how these factors affect diameter of fine roots. The study was conducted in communities located in the Nova Ipixuna, Parauapebas and Pacajá municipalities of Pará state. In each area, nine farms were selected; in each farm were sampled five plots, totaling 135 plots distributed into nine different types of land cover; at each plot, four soil samples were collected to quantify the fine roots, vegetation cover was inventoried, and soil was collected for physical and chemical characterization. Fine roots were separated into four different classes. Principal Component Analysis (PCA) were done for the soil and vegetation matrix and they were compared with the fine root biomass PCA through a co-inertia analysis. Variability was high for fine root biomass data. All land covers exhibited a high proportion of fine roots > 1 mm. The co-inertia analysis showed that the fine root biomass PCA share a common structure with vegetation PCA, with 37% of the variability being explained; however only 9% of the variability was explained by the soil PCA. Our results highlight the importance of roots with diameters < 2 mm for the quantification of root biomass, whereas the biomass of roots > 2 mm was critical to the differentiation among land covers.

ABSTRACT: *O estudo teve como objetivo avaliar o efeito do tipo de cobertura do solo, características edáficas e estrutura da vegetação sobre a biomassa de raízes finas e examinou como esses fatores afetam o diâmetro das raízes finas. O estudo foi realizado em comunidades localizadas nos municípios de Nova Ipixuna, Parauapebas e Pacajá, no estado do Pará. Em cada área, nove fazendas foram selecionadas; em cada fazenda foram amostradas cinco parcelas, totalizando 135 parcelas distribuídas em nove tipos diferentes de cobertura do solo; em cada parcela, quatro amostras de solo foram coletadas para quantificar as raízes finas, a cobertura vegetal foi inventariada e o solo foi coletado para caracterização física e química. As raízes finas foram separadas em quatro classes diferentes. A Análise de Componentes Principais (PCA) foi realizada para a matriz do solo e da vegetação e comparada com a PCA de biomassa de raiz fina através de uma análise de co-inércia. A variação da biomassa de raízes finas foi alta. Todas as coberturas do solo exibiram uma alta proporção de raízes finas > 1 mm. A análise de co-inércia mostrou que a PCA de biomassa de raiz fina compartilha uma estrutura comum com a PCA de vegetação, com 37% da variabilidade sendo explicada; mas somente 9% da variabilidade foi explicada pela PCA de solos. Os resultados destacam a importância de raízes com diâmetros < 2 mm para a quantificação da biomassa radicular, enquanto a biomassa de raízes > 2 mm foi fundamental para a diferenciação entre coberturas de terras.*

KEYWORDS
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1 Introduction

Due to climate change and increasing anthropogenic pressure on forests, the number of studies about the effects of land cover changes on soil quality, floristic composition, plant biomass, productivity and carbon stock is high (Costa et al., 2012; Berenguer et al., 2014; Do Vale et al., 2015; Do Vale et al., 2018). However, studies of the effect of changes in land cover on belowground biomass remain incipient. Fine roots are the principal way for plants to acquire water and plant nutrients, contribute to nutrient cycling in ecosystems, maximize nutrient acquisition in weathered soils such as those in the Amazon, and are highly sensitive to stress by abiotic factors (Freitas et al., 2008; Finér et al., 2011b; Lima et al., 2012).

Fine roots also stand out as the component that most contributes to below-ground carbon fluxes, accounting for up to 75% of annual net primary production in forest ecosystems (Jackson et al., 1997). Roots may have a phenotypic plasticity in response to the environment, like soil moisture, and may increase biomass and decrease its diameter (Metcalfe et al., 2008); may also be related to vegetation cover, since they depend on the species present in the environment (Finér et al., 2011a). A better understanding about changes in root biomass from land cover modifications could help to explain the effect of deforestation on the vegetation and carbon cycle (Jaramillo et al., 2003).

Some studies have examined the close relationship between fine root biomass and edaphic characteristics, vegetation structure and successional stage (Jaramillo et al., 2003; Metcalfe et al., 2008; Finér et al., 2011b; Lima et al., 2012). However, few studies have correlated the roots with different land covers, also taking into account the variations of soil and aboveground vegetation (Jaramillo et al., 2003).

In this study, we quantified and compared the fine root biomass in different land covers types located in different areas of the arc of deforestation region and evaluated the effect of land cover type, chemical and physical properties of soil, and vegetation structure on fine root biomass using multivariate data analysis. We also examined how these factors affect fine root biomass in different diameter classes. Three hypotheses were tested: 1) land cover change affects fine roots biomass and there is less biomass in more extensively managed areas; 2) there is higher fine root biomass in land covers with higher species richness; 3) there is less fine root biomass in soils richer in nutrients. These hypotheses are supported by the hypothesis of species complementarity and theory of resource allocation. The hypothesis of species complementarity assumes that more diverse areas can achieve higher productivity than areas less diverse. This hypothesis was tested in mixed stands in temperate region, poor in species (Brassard et al., 2013). In this study, we expect to provide information about species-rich tropical areas. The theory of resource allocation assumes a lower resource allocation toward the roots in soils with higher nutrient availability (Kozlowski & Pallardy, 2002), as a base to correlate fine root biomass with the physicochemical attributes of soils.

2 Material and Methods

Three areas of family-based agriculture were selected in the region called of the arc of deforestation on Pará state, Brazil. Family-based agriculture is one of the main agents of land cover change in Pará and characterizes the areas studied.

Palmares II Settlement Project (Palmares II), is located 20 Km from the city of Parauapebas, is characterized by pronounced land use dynamics and a significantly fragmented landscape, with small and medium sized patches. All properties have road access, and the houses are located in a village near cultivation fields. Palmares II landscape is the only study area that does not contain conserved forest; however, the forest remnants are an important component that shapes the landscape of the area. Annual crops are more important in this landscape than in the other landscapes (Oszwald et al., 2011).

Agroextractivist Project Praialta Piranheira (Maçaranduba II), is located in Nova Ipixuna municipality, the is characterized by many pastures in different stages of development, and also secondary forests. Remaining forests are concentrated along riverbanks and/or are distant from the smallholder's houses (Oszwald et al., 2011).

The third study area is an area of agricultural colonization that is located on Travessão 338-South (Travessão 338-S) of highway BR-320, in the municipality of Pacajá. This area has experienced recent anthropogenic activity, and its landscape includes extensive areas of conserved forest, which reveals a more homogeneous landscape (Oszwald et al., 2011). It is the only study area that produces perennial crops, *Theobroma cacao* L. associated with *Schizolobium parahyba* (Vell.) S. F. Blake var. *amazonicum* Barneby ex Ducke.

A socio-economic survey carried out with 50 small family farmers helped define which farms were most representative of each agricultural mosaic (De Sartre, 2011). Nine representative farms were selected within each area. Five sampling plots (10 x 50 m) were spaced equally along a transect corresponding either to the longest diagonal of the farm or a roughly north–south axis, totaling 135 plots distributed into nine different types of land cover (Table 1). The plots were distributed within the farm to sample the dominant land covers of the area, previously determined by satellite images. Several plots were utilized to obtain greater spatial variability in the study areas and reduce the uncertainty in the biomass estimation used for carbon calculation as recommended by Breugel et al. (2011).

For to quantify the fine root biomass four soil samples were collected in each plot at 0-30 cm depths, totaling 180 samples per area (nine farms x five plots x four samples = 180 samples per area). The samples were collected between May and July 2008, using a stainless-steel cylinder with a diameter of 5 cm and a height of 10 cm. All collected samples were placed in plastic bags and frozen (-2ºC) until manual root separation was conducted. To separate the fine roots from the soil, each sample was placed in a 0.05 mm mesh cloth bag and washed in running water to remove excess soil. The remaining material after washing was subsequently placed in a plastic tray containing water, and the fine roots were sorted using tweezers.

Roots with a diameter less than or equal to 5 mm were considered to be fine roots and were classified as live (R1 = ≤ 1 mm; R2 = 1-2 mm and R3 = 2-5 mm) or dead (DR = ≤ 5 mm) (Cavelier et al., 1999). Roots with a dark color, reduced flexibility, frequently brittle, were classified as dead (Yavitt & Wright, 2001). After sorting, the roots were placed in paper envelopes, dried at 75ºC for 24 h to 48 h and weighed. Biomass values (g m^{-2}) were calculated using the ratio between the root mass and the area of the cylinder base, as also used by Lima et al. (2010).

Table 1. Types of land cover in three areas of family farms at the arc of deforestation region in the state of Pará, Brazil.

Tabela 1. Tipos de cobertura das três áreas de agricultura familiar estudadas na região do arco do desmatamento no Pará, Brasil.

Land cover type	Description	Palmares II	Maçaranduba II	Travessão 338-S	Total
Conserved forest	Forests with a well-defined vertical structure and no signs of human disturbance	-	8	7	15
Exploited forest	Forests showing signs of disturbance, such as clearings resulting from timber extraction	5	3	16	24
Burned forest	Forests showing signs of fire inside[a]	10	-	-	10
Old secondary forest	Secondary forests with a defined woody upper canopy, older than 12 years	3	9	4	16
Young secondary forest	Secondary forests lacking a defined upper woody stratum, younger than 12 years old	6	4	5	15
Invaded pasture	Pastures with a high abundance of herbaceous individuals and young seedlings of woody species[b]	4	11	6	21
Clean pasture	Pastures with a low density of woody species[b]	7	9	1	17
Annual crops	Rice (*Oryza* sp.), bean (*Vigna* sp.), corn (*Zea mays* L.) and especially cassava (*Manihot esculenta* Cranz) plantations	10	1	2	13
Cocoa plantation	Cocoa (*Theobroma cacao* L.) plantations, generally combined with paricá (*Schizolobium amazonicum* Huber ex Ducke)	-	-	4	4
Total sampling plots		**45**	**45**	**45**	**135**

[a] Occurrence of forest fires is associated with the use of fire to clear the pastures and annual crops areas, sometimes the fire gets out of control and reaches the adjacent forests.

[b] *Brachiaria brizantha* (Hochst. Ex A. Rich.) Stapf was the predominant forage in Palmares II and Maçaranduba II and, *Brachiaria decumbens* Stapf predominated in Travessão 338-S.

A vegetation inventory was conducted in the same 135 plots in which the soil samples for root quantification were collected. Three strata were considered: upper, middle and lower stratum. For the upper stratum, all individuals located within the 10 m × 50 m plot with a diameter at breast height (DBH) > 10 cm were inventoried. For the middle stratum, a 5 m × 50 m subplot was established inside the upper stratum plot and individuals with DBH < 10 cm and height > 2.0 m were inventoried. For the lower stratum, 10 subplots of 1 m × 1 m were distributed at regular intervals at the center of the 10 m × 50 m plot and individuals with 10 cm < height < 2.0 m were inventoried.

All species were collected and identified by comparison at the Herbarium of the Emilio Goeldi Museum of Pará (Museu Paraense Emilio Goeldi). Data on vegetation were collected between April 2008 and July 2008. Species richness per stratum (LowRich, MidRich, UppRich) and density of individuals per stratum (LowDens, MidDens, UppDens) were the variables used in the analysis. Species richness and individual density were represented by the number of species and individuals in each plot, respectively.

In the same 135 plots where fine roots were collected the soil samples were taken for physical and chemical characterization. In each plot two soil samples at 0-10 cm depth were collected, pooled and analyzed for following soil parameters: total sand, clay and silt contents, water infiltration rate (Vi), determined by the simplified infiltration test of Beerkan, bulk density (Da), determined by the cylinder method, pH_{KCl} (in KCl 1M; soil: solution 1:2.5), H^+ and Al^{+3} exchangeable were extracted with 0.5 M solution of $(CH_3COO)_2Ca$, base cations (Ca^{+2}, Mg^{+2}, K^+) extracted with 1 M KCl solution; available P (Mehlich-1 "double acid" extraction method) and NH_4^+ were also determined. Total carbon (C) and nitrogen (N) were determined at a depth of 0-30 cm using a CHNS elemental analyzer (LECO). Soils of the study areas and analytical protocols were more detailed in Grimaldi et al. (2014).

The fine root biomass for each land cover was compared using the nonparametric Kruskal-Wallis test at $p < 0.05$, followed by the multiple comparison test. The contribution of the different diameter classes to the total root biomass was analyzed using the Kolmogorov-Smirnov test (K-S).

Principal Component Analysis (PCA) were performed for each soil and vegetation matrix in addition to the following two co-inertia analyses: i) between fine roots biomass (four absolute values: R1, R2, R3 and DR) and soil (15 variables: total sand, clay, silt, Vi, Da, pH, H^+, Al^{+3}, Ca^{+2}, Mg^{+2}, K^+, P, NH_4^+, C and N) to analyze the relationship between soil physical and chemical characteristics and root biomass; and ii) between fine roots biomass and vegetation structure matrices (6 variables: LowRich, MidRich, UppRich, LowDens, MidDens and UppDens) to analyze the relationship between root biomass and vegetation characteristics. The co-inertia analysis compares the structures revealed in the

PCA analyses, showing whether the co-structure described by the principal axis is similar to the structures described in the analyses performed for each data matrix (Dolédec & Chessel, 1994). The significance of the groups formed in PCA and co-inertia were obtained through the Monte Carlo permutation test at $p < 0.05$, which uses the mean of the scores of each sample point along the ordination gradient. All statistical analyses were performed using the software R (R Foundation for Statistical Computing, Vienna, AT).

3 Results and Discussion

Significant differences in total fine root biomass were observed for the different land covers (U = 48.5; $p < 0.0001$). The lowest total fine roots biomass was observed in annual crops (189.1 g m^{-2}), and the highest in conserved forests (516.3 g m^{-2}) (Table 2). However, the variability in the data was high, with coefficients of variation ranging between 19% for conserved forests to 60% for annual crops. Conserved and exploited forests and old secondary forests displayed similar values of total fine roots biomass. The conversion from conserved forest to annual crops and clean pastures resulted in a loss of 63% and 39% of total fine root biomass, respectively.

Table 2. Fine root biomass (g m^{-2}) by diameter classes (mm) per type of land cover (mean ± standard deviation). Fine roots diameter classes: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = dead roots (≤ 5 mm); Total = R1 + R2 + R3 + DR.

Tabela 2. Biomassa de raízes finas (g m^{-2}) por classe de diâmetro (mm) por tipo de cobertura da terra (média ± desvio padrão). Classes de diâmetro das raízes finas: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = raízes mortas (≤ 5 mm); Total = R1 + R2 + R3 + DR.

Land cover types	R1	R2	R3	DR	TOTAL*
Conserved forest	248.2 ± 7.3	103.8 ± 7.3	137.3 ± 20.9	27.1 ± 4.3	516.3 ± 25.8a
Exploited forest	252.4 ± 20.1	89.5 ± 7.7	105.4 ± 14.1	43 ± 8.1	490.3 ± 37.1ab
Burned forest	159.2 ± 11.7	41.1 ± 5.6	83.7 ± 17	35.5 ± 8	319.6 ± 26.5abc
Old secondary forest	253.6 ± 22.5	67.8 ± 8.4	113.3 ± 23.6	30 ± 6.8	464.7 ± 49.9ab
Young secondary forest	215.4 ± 22.6	52.8 ± 7.7	53.9 ± 11	24.8 ± 6.2	346.9 ± 34.6abc
Invaded pasture	284.6 ± 35.8	32.1 ± 4.4	44 ± 7.6	14 ± 2.9	374.6 ± 38.5abc
Clean pasture	261.6 ± 32.8	28.7 ± 6.2	11.5 ± 5.7	13.7 ± 3.1	315.5 ± 35.7bc
Anual crops	108.7 ± 25.9	22.6 ± 6.8	26.4 ± 10.6	31.5 ± 6.3	189.1 ± 30.3c
Cocoa plantation	113.3 ± 21.2	41.4 ± 7.9	48.3 ± 12.5	43.1 ± 11.9	246.1 ± 33abc

*Values followed by the same letters means statistical similarity between types of land cover (Kruskal-Wallis test, $p > 0.05$).

*Valores seguidos por letras iguais mostram semelhança estatística entre os tipos de cobertura da terra (Teste de Kruskal-Wallis, p > 0,05).

The proportions of fine root biomass for the different diameter classes were also affected by the land cover types (K-S, $p < 0.05$) (Figure 1). All land covers types exhibited a high proportion of R1; However, significant differences (K-S, $p < 0.01$) were observed in clean pastures (82.91%) and invaded pastures (75.97%) when compared with the others land cover types (mean of approximately 50%). Cacao plantations, annual crops, burned and exploited forests showed the highest proportion of DR in relation to total fine root biomass (17.5, 16.6, 11.1 and 8.8%, respectively). A more equitable distribution of the different root diameter classes was observed for cocoa plantations.

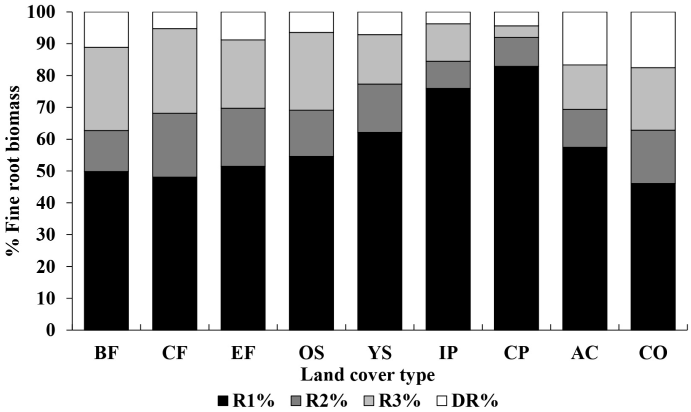

Figure 1. Proportion of the fine root biomass by diameter classes and land cover type. BF = Burned forest; CF = Conserved forest; EF = Exploited forest; OS = Old secondary forest; YS = Young secondary forest; IP = Invaded pasture; CP = Clean pasture; AC = Annual crop; CO = cocoa plantation. Fine roots diameter classes: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = dead roots (≤ 5 mm).

Figura 1. Proporção da biomassa de raízes finas por classe de diâmetro e tipo cobertura do solo. BF = Floresta queimada; CF = Floresta conservada; EF = Floresta explorada; OS = Floresta secundária velha; YS = Floresta secundária jovem; IP = Pastos invadidos; CP = Pastos limpos; AC = Culturas anuais; CO = Plantação de cacau. Classes de diâmetro das raízes finas: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = raízes mortas (≤ 5 mm).

The first two axes of PCA explained 82.5% of total data variance; axis 1 explained 67.95% and axis 2 explained 14.6% of variance (Figure 2a). Fine roots biomass was influenced by different land cover types (39%) (Monte Carlo test, $p < 0.001$); sampling grouping in the factorial plan (Figure 2b) reflects the land cover influence on the quantity of fine root biomass in different diameter classes.

Root biomass class R3 contributed 84.5% in the formation of groups in axis 1, highlighting three land cover groups: group 1, highest root biomass class R3, formed by primary forests (conserved, exploited and burned) and old secondary forests; group 2, intermediate biomass, formed by young secondary forests, cacao plantations and invaded pastures; and, group 3, lowest biomass, formed by annual crops and clean pastures (Figure 2b).The axis 2 of PCA highlighted the contribution of dead roots (90.2%) in the formation of groups, in which cacao plantations, annual crops, burned and exploited forests showed positive correlation (Figure 2a, b). Total fine root biomass also influenced the group formation of axis 1, since all root variables were positioned to the left of this axis (Figure 2a). In this case, primary forests and old secondary forests were separated from pastures and annual crops (Figure 2b). This results confirm the hypotheses that land cover change affects fine roots biomass, with less biomass in more extensively managed areas.

The similarity between the total biomass of fine roots in primary forests and young and old secondary forests may be attributed to the rapid recovery of root biomass in

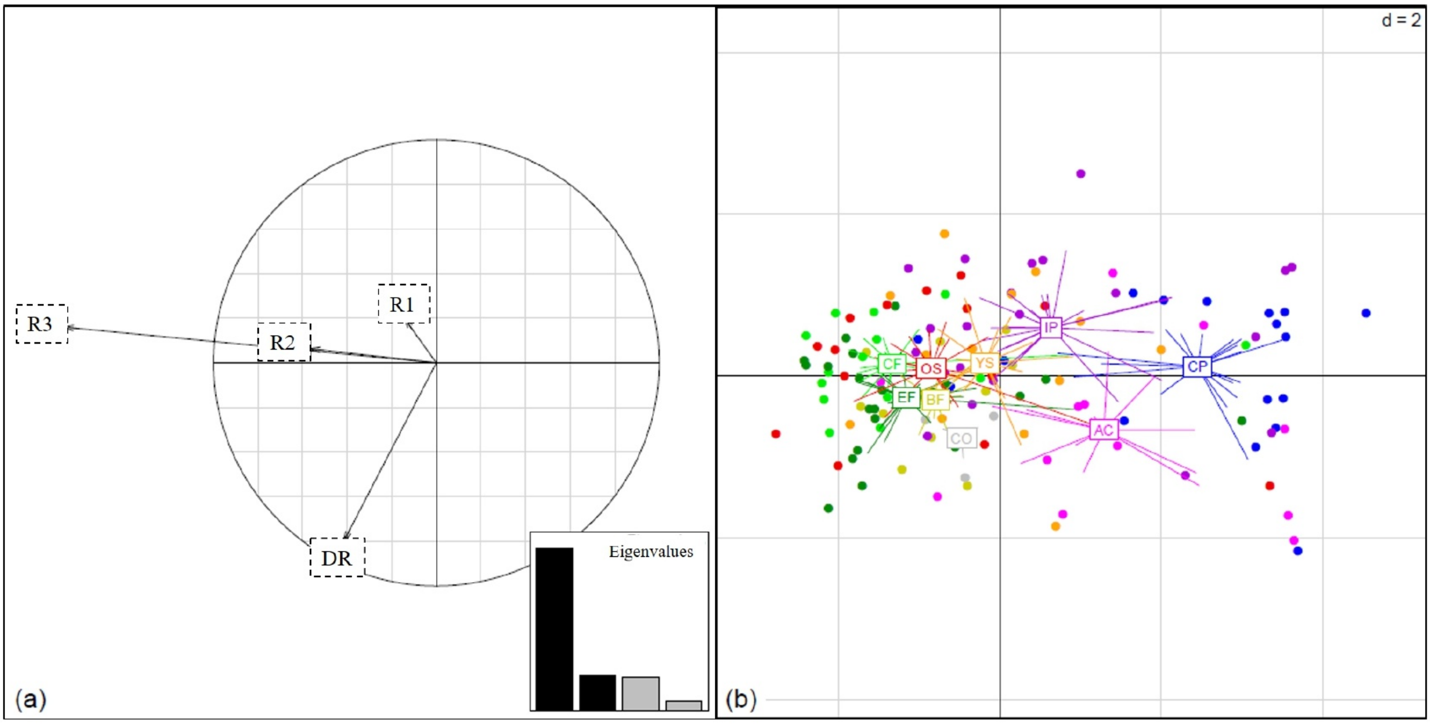

Figure 2. Ordination of the first and second axes of the principal component analysis: (a) Correlation circle of fine root diameter classes: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = dead root (≤ 5 mm)); (b) Ordination of the 135 plots grouped per land cover type (BF = Burned forest; CF = Conserved forest; EF = Exploited forest; OS = Old secondary forest; YS = Young secondary forest; IP = Invaded pasture; CP = Clean pasture; AC = Annual crop; CO = cocoa plantation.

Figura 2. Ordenação da análise de componente principal: (a) Correlação circulo das classes de diâmetro das raízes finas: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = raízes mortas (≤ 5 mm)); (b) Ordenação das 135 parcelas agrupadas por tipo de cobertura do solo (BF = Floresta queimada; CF = Floresta conservada; EF = Floresta explorada; OS = Floresta secundária velha; YS = Floresta secundária jovem; IP = Pastos invadidos; CP = Pastos limpos; AC = Culturas anuais; CO = Plantação de cacau).

these environments, which indicates the process of regeneration during forest succession (Jaramillo et al., 2003). Other authors did not observe differences in fine root biomass between secondary forests of different ages (Cavelier et al., 1996; Lima et al., 2012). Our results show that this similarity is limited to root biomass classes R1 and R2, since young secondary forests displayed a low proportion of R3 biomass compared to primary forests and old secondary forests and similar proportion for R1 and R2 classes. This pattern was also observed for pastures and annual crops, which indicates that changes in land cover can cause a significant loss of roots with diameters > 2 mm. The use of fire in annual crops and pastures may have influenced a lower total root biomass and a higher proportion of dead roots for these land covers; similar result was found by Román & Cuesta (2011).

The greatest contribution to the root biomass was obtained from roots with a diameter less than 1 mm. This significant input was also observed in other studies (Metcalfe et al., 2008; Leão et al., 2014). Despite their importance, roots with a diameter less than 1 mm were not useful for differentiating the land cover types. The difference in the fine root biomass of the land covers was better explained by the biomass of class R3, because different from R1 it was more variable between land cover, showing the impact of the change of land cover in roots with larger diameters.

The co-inertia analysis to evaluate the soil effect on fine root biomass showed significant co-variance between the roots and soil matrices; however, the correlation coefficient was very low (correlation coefficient = 0.09; Monte Carlo test, $p = 0.003$). The first two axes explained 92.5% of the variability in the data (axis 1 = 72.3%; axis 2 = 20.2%). Within the root matrix root biomass class R3 explained 67.2 % of the variances of axis 1; soil matrix variables with higher contribution to the axis 1 were Vi (24%), pH (18.6%), Ca^{+2} (18.3%) and Al^{+3} (14.6%) (Table 3; Figure 3a). The ordination of samples in the axis 1 showed a gradient of conservation in the vegetation covers (Figure 3b). This axis influenced more than 65% the variables R2, R3 and DR and more than half of the chemical characteristics of the soil (Table 3).

Land cover types with the highest fine root biomass in classes R2, R3 and DR were positively correlated to soils with high contents of Al^{+3} and Vi (conserved, exploited and burned forests and old secondary forests); young secondary forests, with intermediate values, at the center of the axis; a group with pastures and annual crops, with lower root biomass were positively correlated to soils with high pH and Ca^{+2} contents (Figure 3b). We could not identify the ordering of the cocoa plantation samples. Axis 2 was mainly formed by root biomass classes R1 and R2, which were positively associated with sand and Da. The total carbon (C) and nitrogen (N) contents were negatively related to root biomass classes R1 and R2 (Figure 2a). The axis 2 highlighted a gradient of root diameter associated mainly with the soil texture. However, we could not

Table 3. Percent contribution of fine roots, soil and vegetation variables to the variance in the co-inertia axes, and the percent influence of the axes on the variables. Fine roots diameter classes: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = dead root (≤ 5 mm).

Tabela 3. Porcentagem de contribuição das raízes finas, variáveis do solo, e da vegetação para a variância explicada nos eixos da co-inercia e a porcentagem de influência dos eixos sobre as variáveis. Classes de diâmetro: R1 = ≤ 1mm; R2 = 1-2mm; R3 = 2-5 mm; DR = raízes mortas (≤ 5 mm).

Co-inertia	Variables	Contribution variable to the variance in the axes (%)		Influence of the axes on the variables (%)	
		Axis 1	Axis 2	Axis 1	Axis 2
Fine roots x Soil (Coefficient of correlation = 0.09; p = 0.003)	**R1**	1.00	43.62	7.56	92.44
	R2	22.26	39.32	66.94	33.06
	R3	67.17	15.02	94.12	5.88
	DR	9.57	2.04	94.38	5.62
	Clay	0.79	19.25	12.76	87.24
	Silt	2.59	0.20	97.89	2.11
	Sand	0.32	20.63	5.19	94.81
	pH	18.63	1.31	98.06	1.94
	Al^{+3}	14.53	0.63	98.80	1.20
	Ca^{+2}	18.24	3.71	94.62	5.38
	Mg^{+2}	2.33	0.01	99.93	0.07
	K^{+}	3.28	1.74	87.06	12.94
	P	0.90	3.67	46.69	53.31
	NH_4^{+}	6.69	3.78	86.36	13.64
	C	0.01	11.17	0.42	99.58
	N	1.43	10.39	32.93	67.07
	Da	6.32	12.64	64.12	35.88
	Vi	23.96	10.86	88.76	11.24
Fine roots x Vegetation (Coefficient of correlation = 0.37; p = 0.001)	**R1**	0.16	31.20	41.73	58.27
	R2	24.38	10.01	99.71	0.29
	R3	69.07	16.93	99.83	0.17
	DR	6.39	41.85	95.60	4.40
	Lower density	1.30	2.34	98.75	1.25
	Middle density	35.20	30.82	99.39	0.61
	Upper density	23.18	33.64	98.99	1.01
	Lower richness	1.60	0.45	99.80	0.20
	Middle richness	21.81	12.12	99.61	0.39
	Upper richness	16.91	20.63	99.15	0.85

identify any group formation (Figure 3b).

The gradient of vegetation conservation along axis 1 of the co-inertia between roots and soils showed loss of biomass associated with water infiltration rate (Vi), considering that in the studied areas water infiltration rate is more influenced by land cover than traits inherent to the soil, as texture, can say that the conversion of forests to land cover with little or no trees has a negative influence on the water infiltration rate and that this is also associated with the importance of the root system in this process (Grimaldi et al., 2014). As for bulk density, as expected, the higher bulk density was associated with pastures. Soil bulk density emerge, along with sand and clay, as a variable that influences fine root diameter; it is positively related to biomass classes R1 and R2, characterizing pastures.

The positive co-variation in the biomass of roots with diameters ≤ 2 mm (R1 and R2) with sandier soils may be explained by the lower resistance to root penetration in these soils. Conversely, the biomass of R3 roots positively co-varied with clayey soils, in which the roots tend to increase in diameter as a strategy to penetrate these soils. This close relationship between soil texture and root biomass and morphology has been observed in other studies of the Amazon region (Metcalfe et al., 2008). However, the land cover in the study areas exhibits minimal or no influence on the soil inherent properties, such as texture (Grimaldi et al., 2014).

Although the contribution of pH, Al^{+3} and Ca^{+2} to the formation of axis 1 was high, due to low correlation between root and soil matrices, we believe that higher fine

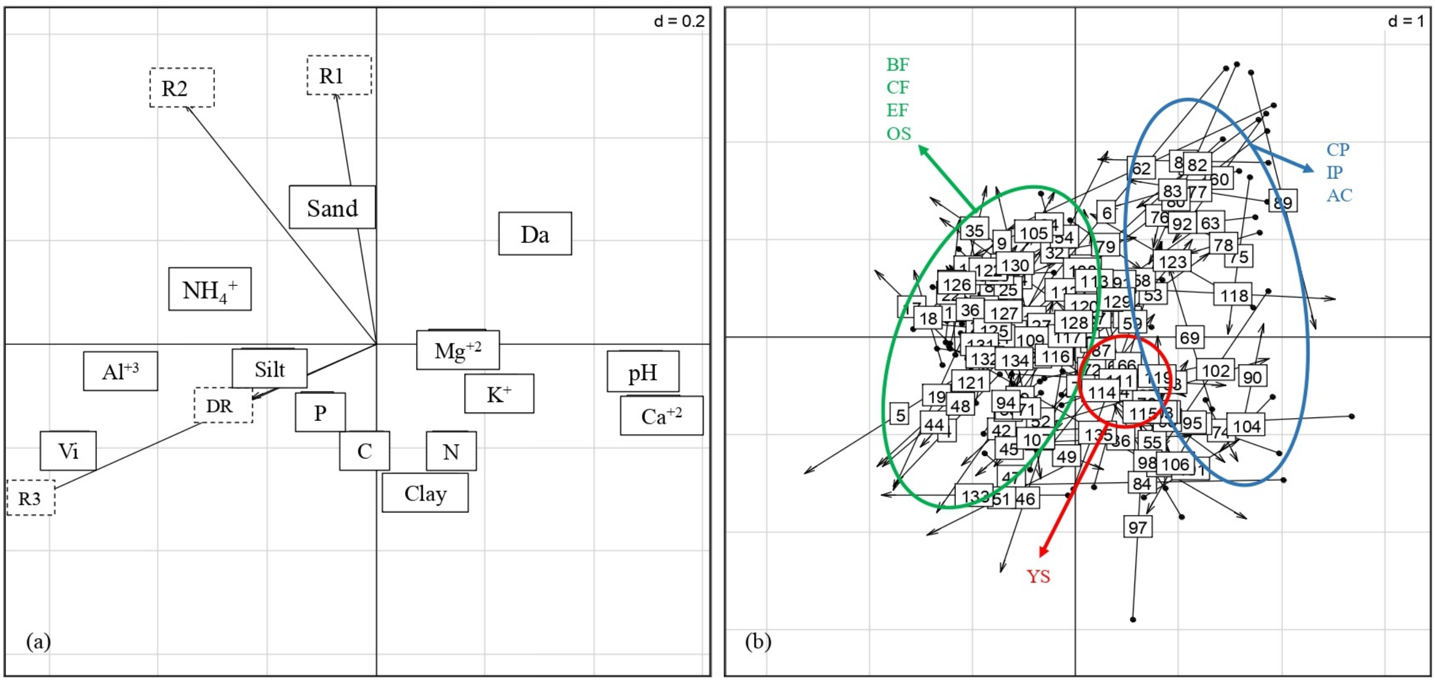

Figure 3. Ordination of the first and second axes of the analysis of co-inertia between fine root biomass and physical and chemical soil characteristics: (a) Ordination of fine root and soil variables; (b) Ordination of the 135 plots grouped per land cover type (BF = Burned forest; CF = Conserved forest; EF = Exploited forest; OS = Old secondary forest; YS = Young secondary forest; IP = Invaded pasture; CP = Clean pasture; AC = Annual crop; CO = cocoa plantation).

Figura 3. Ordenação dos dois primeiros eixos da análise de co-inércia entre biomassa de raízes finas e características físicas e químicas dos solos: (a) Ordenação das raízes finas e variáveis dos solos; (b) Ordenação das 135 parcelas agrupadas por tipo de cobertura do solo (BF = Floresta queimada; CF = Floresta conservada; EF = Floresta explorada; OS = Floresta secundária velha; YS = Floresta secundária jovem; IP = Pastos invadidos; CP = Pastos limpos; AC = Culturas anuais; CO = Plantação de cacau).

root biomass found in soils that are more acid (represented by primary forests and old secondary forests) is related to land cover, instead of being related to the consequences that acidity may have on nutrient absorption.

Fine root biomass was more influenced by the land cover types and the characteristics of the vegetation (in this case, species richness and plant density) compared with the physical and chemical soil characteristics, once that correlation between soil attributes and fine roots is low and this result did not allow the confirmation of the hypothesis that there is less fine root biomass in soils richer in nutrients. Similar result, in the same plots studied, was shown by Costa et al. (2012) for above ground biomass; and this indicates that factors that affect aboveground biomass also affect fine root biomass. The weak correlation between the soil and root matrices may be attributed to the fast-paced dynamics that occur at the root system after aboveground changes. Bengough et al. (2006) suggest that the root system is influenced not only by soil conditions but also by the communication with other parts of the plant, especially when the soil is spatially heterogeneous in terms of nutrients.

The co-inertia analysis to evaluate the effect of vegetation structure on fine root biomass (Figure 4) indicated a significant co-variance between the root and vegetation structure matrices, which shared approximately 37% of the data variance (p = 0.001). Axis 1 explained 99.2% of the variability in the data. The variables responsible for the greatest contributions to the variance of axis 1 were root class R3 (R3 = 69.1%) from the root matrix, the plant density and richness of the middle stratum (35.2% and 21.8%, respectively) and the density of the upper stratum (23.2%) from the vegetation structure matrix (Table 3; Figure 4a). Axis 1 highly influenced all variables in the two matrices (Table 3) and showed a gradient of the vegetation structure conservation (Figure 4b). Ordination of samples in axis 1 formed three groups: (1) a group formed by primary forests, old secondary forest and cocoa plantations, which are positively correlated with all root classes and the density and richness of the upper and medium strata; (2) young secondary forests isolated at the center; (3) a group formed by the pastures and annual crops to the right, which are negatively correlated with the density and richness of the upper and medium strata (Figure 4a, b).

Our results confirm the hypothesis that land covers types with a predominance of tree species, such as primary forests and old secondary forests, significantly contribute to fine root biomass. In this study, a positive relationship between species richness and root biomass was observed, as also observed in Brassard et al. (2013) and Lei et al. (2012) studies. The land cover gradient formed on axis 1 of the co-inertia analysis between the root and vegetation matrices showed that fine root biomass significantly decreased for no forest covers. This decrease was distinctly related to a reduction in species richness and plant density of the middle and upper canopy caused by a

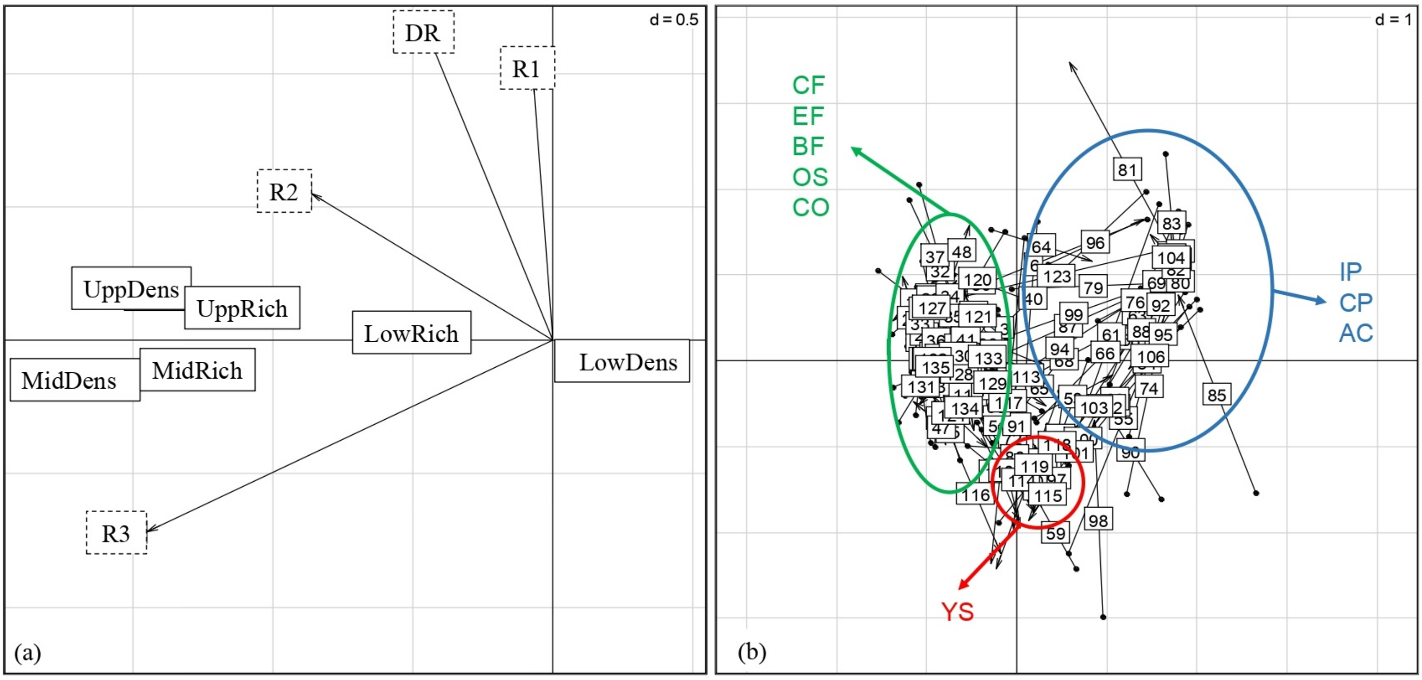

Figure 4. Ordination of the first and second axes of the co-inertia analysis between fine root biomass and vegetation structure: (a) Ordination of fine root and vegetation variables; (b) Ordination of the 135 plots grouped per land cover type (BF = Burned forest; CF = Conserved forest; EF = Exploited forest; OS = Old secondary forest; YS = Young secondary forest; IP = Invaded pasture; CP = Clean pasture; AC = Annual crop; CO = cocoa plantation).

Figura 4. Ordenação dos dois primeiros eixos da analise de co-inercia entre biomassa de raízes finas e estrutura da vegetação: (a) Ordenação das raízes finas e variáveis da vegetação; (b) Ordenação das 135 parcelas agrupadas por tipo de cobertura do solo (BF = Floresta queimada; CF = Floresta conservada; EF = Floresta explorada; OS = Floresta secundária velha; YS = Floresta secundária jovem; IP = Pastos invadidos; CP = Pastos limpos; AC = Culturas anuais; CO = Plantação de cacau).

change in land cover. Hertel et al. (2009) observed that fine root production decreased considerably with increased vegetation disturbance and attributed this decrease to the change in vegetation structure.

The higher root biomass observed for clean pastures compared with annual crops may be attributed to higher plant density at the lower stratum in pastures and the root architecture of grasses, which significantly contributes to the biomass of finer roots (diameter < 1 mm). The positive correlation between plant density of the middle and upper strata with class R2 and R3 root biomass indicates that land covers with a predominance of tree species, such as primary and secondary forests, increase the biomass of roots with diameters greater than or equal to 2 mm.

4 Conclusion

The land cover types affected fine root biomass, which decreased with increasing disturbance. The conversion of forest into less complex land covers such as pastures and annual crops, decreases the fine root stock, and the biomass of roots with diameters > 2 mm is more negatively affected by this process. Types of land cover that conserve tree species and exhibit high diversity produce greater quantities of fine root biomass. Vegetation characteristics (density and richness) were more determinants than soil characteristics for the fine root biomass. Our results highlight the importance of roots with diameters < 2 mm for the quantification of root biomass, whereas the biomass of roots > 2 mm was critical to the differentiation among land covers due to the rapid recovery of very fine roots.

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