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RETRANSLOCAÇÃO DE NUTRIENTES FOLIARES DE ESPÉCIES ARBÓREAS DE *TERRA FIRME* DA AMAZÔNIA CENTRAL

JULYANE STEPHANIE PIRES DOS SANTOS

Manaus, Amazonas
Julho, 2020

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Orientador: Dr. Carlos Alberto Nobre Quesada
Coorientadora: Dra. Sabrina Garcia

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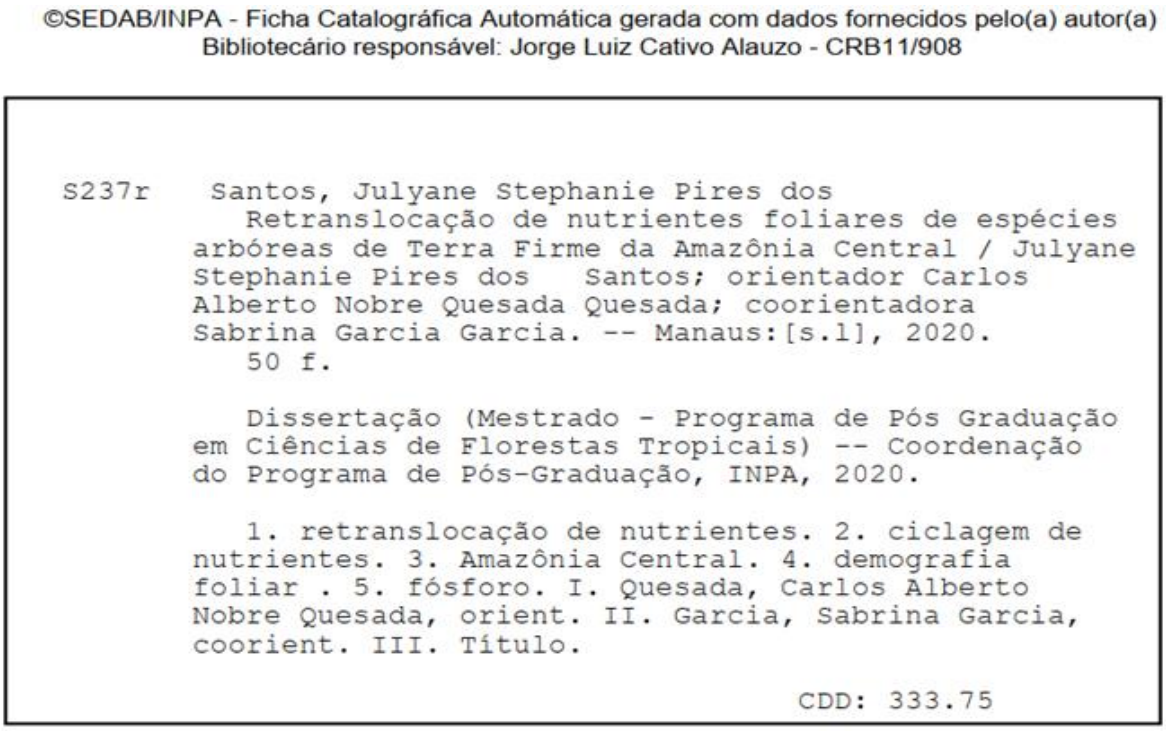

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Sinopse

O foco do trabalho é insvestigar a retranslocação de nutrientes em uma floresta madura na Amazônia Central e como fatores internos e externos, como a concentração de nutrientes foliares, a longevidade foliar e a posição da copa podem influenciar essa estratégia importante de ciclagem interna de nutrientes. Nossos dados sugerem que a concentração de nutrientes influenciou positivamente a retranslocação da maioria dos nutrientes estudados. Além disso, os nutrientes mais retranslocados nessa floresta madura foram P e K, demonstrando que possivelmente esses nutrientes são os mais limitantes nesse ambiente.

Palavras-chave: retranslocação, nutrientes foliares, Amazônia Central, ciclagem de nutrientes.

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“It is good to have an end to journey toward, but it is the journey that matters in the end.”

(Ernest Hemingway)

Resumo

A retranslocação de nutrientes ocorre antes da abscisão foliar, havendo o transporte dos nutrientes para outras partes da planta. É uma estratégia importante na conservação de nutrientes e influencia a ciclagem de nutrientes nos ecossistemas. No entanto, nossa compreensão do que influencia os processos de retranslocação em árvores tropicais é limitada. Desse modo, para melhorar nosso entendimento desses processos, estudamos a retranslocação foliar de nove macro e micronutrientes em uma comunidade florestal. O objetivo foi investigar os efeitos da concentração de nutrientes de folhas maduras, longevidade foliar e posição do dossel na retranslocação de nutrientes em uma floresta de *terra firme* na Amazônia Central. Para isso, determinamos a concentração de nutrientes nas folhas em diferentes idades e a eficiência e proficiência da retranslocação nessa comunidade. O local do estudo foi na área do AmazonFACE, onde foram utilizadas duas torres para acesso a copa das doze árvores estudadas. As folhas senescidas usadas foram coletadas quinzenalmente entre agosto de 2018 a dezembro de 2019. Encontramos uma forte diminuição de P e K em diferentes idades foliares, e tendência contrária para Ca, Fe, Zn e Mn que aumentaram com a idade foliar. Além disso, verificamos que a concentração de nutrientes de folhas maduras estava correlacionada positivamente com a retranslocação de C, N, P, Fe e Zn. Verificamos que a longevidade foliar estava positivamente correlacionada com a maioria dos nutrientes, com exceção de Ca, Fe, Zn e Mn. Entretanto, a posição do dossel foi correlacionada positivamente apenas com a retranslocação de C, K e Zn. Nossos resultados demonstraram que nessa floresta, P e K foram os nutrientes mais retranslocados (33.24% e 42.03%, respectivamente) e que dependendo do nutriente, alguns processos podem afetar a retranslocação mais do que outros. Nossos resultados também enfatizam a importância de entender a interação de diferentes espécies na ciclagem de nutrientes, o que também deve refletir no desempenho do crescimento individual. A retranslocação é um mecanismo fundamental de conservação de nutrientes em florestas tropicais com baixo teor de nutrientes e deve ser considerada na previsão de cenários futuros.

Palavras-chave: retranslocação; nutrientes foliares; Amazônia Central; ciclagem de nutrientes; fósforo; floresta tropical; folhas senescentes; eficiência na retranslocação; proficiência; demografia foliar.

Abstract

Nutrient retranslocation occurs before leaf abscission, with nutrients being translocated to other parts of the plant. It is an important strategy for nutrient conservation and influences nutrient cycling in ecosystems. However, our understanding of what influences retranslation processes in tropical trees is limited. Thus, to improve our understanding of these processes, we studied the retranslocation of nine macro and micronutrients in a tree community. The objective was to investigate the effects of leaf nutrient concentration in mature leaves, leaf longevity and canopy position in the retranslocation of nutrients in a lowland forest in central Amazonia. For this, we determined leaf nutrients concentration at different leaf ages and the retranslocation efficiency and proficiency in the community. The study was carried out at the AmazonFACE research area, where two towers were used to access the canopy of the twelve tree species studied. The senescent leaves of individual trees were collected every fifteen days from August 2018 to December 2019. We found a strong decrease in P and K at different leaf ages and a contrary tendency for Ca, Fe, Zn and Mn which increased with leaf age. In addition, we found that the nutrient concentration in mature leaves was positively correlated with the retranslocation of C,N, P, Fe and Zn. In addition, we observed that leaf longevity was positively correlated with most nutrients, except for Ca, Fe, Zn and Mn. However, the canopy position was positively correlated only with C, K and Zn retranslocation. Our results showed that in this forest P and K were the most retranslocated nutrients (33.24% and 42.03%, respectively) and that some processes can affect specific nutrient retranslocation in different ways. Our results also emphasize the importance of understanding the interaction of different species in nutrient cycling which should also reflect on individual growth performance. Retranslocation is a fundamental nutrient conservation mechanism in low nutrient tropical forests and should be considered when predicting future scenarios.

Keywords: retranslocation; leaf nutrient; Central Amazon; nutrient cycling; phosphorus; tropical forest; senescent leaves; retranslocation efficiency; proficiency; leaf demography.

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Introdução

As florestas tropicais representam aproximadamente um terço do estoque global de carbono (C) terrestre (Phillips et al. 2009, Pan et al. 2011, Carvalhais et al. 2014). A Amazônia representa a maior região contínua de florestas tropicais, armazenando cerca de 150 Peta gramas de C (Feldpausch et al. 2012) e fornecendo importantes serviços ecossistêmicos como alta biodiversidade e regulação do clima (Pan et al. 2011, Zhao e Running 2010). Os solos ao longo da Bacia Amazônica variam muito em geologia e disponibilidade de nutrientes, com um claro gradiente de fertilidade aumentando de leste para oeste, resultando em feedbacks com produtividade de biomassa que também variam ao longo da Bacia (Aragão et al. 2009, Cleveland et al. 2011; Quesada et al. 2012).

Há a predominância de Acrisols e Ferralsols ao longo da parte central e oriental da Bacia Amazônica, que são solos antigos e altamente intemperizados que cobrem cerca de 60% da Bacia Amazônica, no entanto nos 40% restantes encontram-se solos de nível pedogenético bastante variado, com solos jovens e pouco desenvolvidos (Quesada et al. 2011). A concentração de nutrientes derivados da rocha, como fósforo (P), cálcio (Ca), magnésio (Mg) e potássio (K), tendem a diminuir ao longo do desenvolvimento (idade) dos solos, tornando-se gradativamente lixiviados e menos disponíveis, limitando sua disponibilidade para as plantas (Quesada et al. al. 2010, 2011).

A limitação dos nutrientes do solo pode afetar a produtividade das florestas tropicais (Malhi et al. 2004, Quedada et al. 2012). Estudos demonstram que a produtividade primária líquida aumenta com o status de P do solo (Aragão et al. 2009). Quesada et al. (2010) encontraram uma correlação positiva entre a produtividade de madeira e os teores de P do solo nas florestas amazônicas. Dados sobre a disponibilidade de P têm sido cruciais para o entendimento das variações na produtividade das florestas amazônicas (Mercado et al. 2011). Esses resultados apoiam modelagens globais, que previram que nitrogênio (N) e P limitariam a produtividade futura e a capacidade de armazenamento de C terrestre (Wieder et al. 2015, Fleischer et al. 2019). Diante de deficiências nutricionais, diferentes estratégias das plantas evoluíram para otimizar a aquisição e o uso da maioria dos macro e micronutrientes, afetando fortemente o desempenho das plantas (Maillard et al. 2015).

Em ambientes onde a disponibilidade de nutrientes nos solos é baixa, vários mecanismos são adotados para aumentar a eficiência com que os nutrientes são utilizados pelas plantas. Vitousek (1982,1984) sugere que o uso de nutrientes pode ser considerado eficiente quando uma maior biomassa for produzida por unidade de nutriente contido na biomassa. Existem processos que aumentam a eficiência com que os elementos são ciclados e reabsorvidos no ecossistema, favorecendo sua manutenção e reduzindo suas perdas. A retranslocação de nutrientes (também chamada de reabsorção de nutrientes) (Aerts 1996, Chapin 1980, Eckstein et al. 1999, Zhang et al. 2015) é fundamental para a economia de nutrientes das plantas, processo pelo qual os nutrientes passam das folhas senescentes para órgãos de armazenamento ou tecidos em crescimento, reduzindo os custos de construção das folhas, liberando as plantas da dependência estrita da absorção de nutrientes do solo (Rea et al. 2018). A retranslocação é um componente essencial das estratégias de conservação de nutrientes e, portanto, influencia muitos processos em ecossistemas florestais, incluindo a ciclagem de C e a eficiência no uso de recursos.

Alguns estudos abordaram padrões espaciais e temporais de retranslocação de nutrientes e sua relação com processos ecofisiológicos das plantas (Chapin e Moilanen 1991, Del Arco et al. 1991, Escudero et al. 1992, Niinemets e Tamm 2005). As concentrações foliares de alguns nutrientes em tecidos maduros e jovens, geralmente são mais altas porque esses tecidos demandam mais recursos para seu rápido crescimento (Mattson 1980, Harper 1989, Zhao et al. 2016, Prietro e Querejeta 2020). O perfil vertical do extrato florestal também pode influenciar nas características foliares (Carswell et al. 2000, Domingues et al. 2005, Kosugi et al. 2012, Weerasinghe et al. 2014, Kenzo et al. 2015), visto que ao longo do perfil vertical de florestas tropicais, a estrutura e composição da vegetação promovem heterogeneidade na disponibilidade dos recursos, sendo destacável a redução exponencial da irradiância solar a partir do dossel em direção ao sub-bosque (Kenzo et al. 2015).

A capacidade de retranslocação pode ser medida como eficiência ou proficiência, sendo a eficiência a proporção de nutrientes reabsorvidos de folhas senescentes em relação aos nutrientes de folhas verdes. A proficiência de retranslocação mede a capacidade de reabsorção final da folha e representa o limite bioquímico da retranslocação, onde indivíduos mais proficientes têm níveis mais baixos de nutrientes nas folhas senescentes (Killingbeck 1996). Embora eficiência e proficiência sejam características complementares, Killingbeck (1996) argumenta que a proficiência influencia diretamente na qualidade da matéria orgânica que será eventualmente ciclada e voltará para o ecossistema. Material com alta proficiência, portanto, resulta em menores concentrações finais de nutrientes e provavelmente a taxa de decomposição desse material será mais lenta (Killingbeck 1996).

Dado que a disponibilidade de N e P pode influenciar a resposta global do ciclo de C às mudanças ambientais (van Groenigen et al. 2006, Matear et al. 2010, Wassen et al. 2013), observou-se que as concentrações de N podem ser mais sensíveis a CO_2 elevado do que as concentrações de P, algo que foi observado principalmente em ecossistemas temperados, com baixos teores de N nos solos, mas onde P é usualmente mais disponível (Feng et al. 2015, Huang et al. 2015). Entretanto, a importância da dinâmica de P em ambientes de CO_2 elevado é menos clara (Ågren, 2008, Goll et al. 2012, Zhang et al. 2014) o que afeta florestas como a Amazônia, que possuem baixa concentração deste elemento em ao menos 60% de seus solos (Quesada et al. 2010).

Devido a uma possível maior demanda de crescimento, o aumento de CO_2 pode alterar a eficiência ou a proficiência da retranslocação de nutrientes, influenciando a qualidade da serapilheira e consequentemente a ciclagem de nutrientes (Dijkstra et al. 2012, Crous et al. 2019). Fleisher et al. (2019) previram que a resposta da floresta Amazônica depende das interações e das estratégias de aquisição e uso de fósforo entre os indivíduos e até que ponto esses processos podem ser regulados sob CO_2 elevado. Estudos destacam a necessidade de explorar ainda mais o papel dos nutrientes para melhorar a precisão dos modelos globais de carbono-clima (Cleveland et al. 2011).

A retranslocação de nutrientes dos tecidos vegetais é uma estratégia fundamental para a conservação de nutrientes nas plantas. No entanto, a compreensão dos processos de retranslocação de nutrientes em árvores tropicais é limitada. Desse modo, neste trabalho investigamos os efeitos da concentração de nutrientes em folhas maduras, longevidade foliar e posição do dossel para entender o processo de retranslocação de nutrientes em árvores de uma floresta de *terra firme* na Amazônia Central, caracterizada por solos com baixas concentrações de P e cátions. Os objetivos específicos deste estudo foram: (a) determinar a concentração de nutrientes nas diferentes idades das folhas; e (b) estimar a eficiência na retranslocação de nutrientes no nível da comunidade e do ecossistema e proficiência de uma floresta na Amazônia Central. Neste trabalho as hipóteses levantadas foram que a retranslocação é (1) influenciada pela concentração de nutriente nas folhas; (2) influenciada pela longevidade foliar; (3) influenciada pela a posição do dossel; e alternativamente (4) a retranslocação de nutrientes não varia na comunidade estudada, devido à baixa disponibilidade de P no solo.

Capítulo único

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AUTHORS: Julyane Stephanie Pires dos Santos[1], Sabrina Garcia[2], Laynara Figueiredo Lugli[2], Bruno Takeshi[2], Ana Gracy de Oliveira[1], Juliane Cristina Gomes Menezes[2], Tomas Ferreira Domingues[3], David M. Lapola[4], Carlos Alberto Quesada[1,2].

[1]Programa de Pós-Graduação em Ciências de Florestas Tropicais. Instituto Nacional de Pesquisas da Amazônia (INPA). Av. André Araújo, 2936, Manaus, Brasil. 69011-970, julyane.florestal@gmail.com, Telefone: +55 (92) 3643-1911

[a]gracyribeiro07@gmail.com, Telefone: +55 (92) 3643-1911

[b]quesada.beto@gmail.com, Telefone: +55 (92) 3643-1818

[2] Coordenação de Pesquisa em Dinâmica Ambiental. Instituto Nacional de Pesquisas da Amazônia (INPA). Av. André Araújo, 2936, Manaus, Brazil. PO box 478, 69011-970, [a]sabrinagarcia.sg@gmail.com, Telefone: +55 (92) 3643-1986

[b]laynaralugli@gmail.com, Telefone: +55 (92) 3643-1986

[c]brunotakeshi@gmail.com, Telefone: +55 (92) 3643-1986

[d]julianecgm@gmail.com, Telefone: +55 (92) 3643-1911

[3]Universidade de São Paulo, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto. Av. Bandeirantes, 3900 - Depto. de Biologia. Ribeirão Preto, Brasil. 14040-901, tdomingu@gmail.com, Telefone: +55 (16) 3315-3814

[4]Centro de Pesquisa Meteorológica e Clima Aplicada à Agricultura, Universidade de Campinas, Campinas, SP 13083-886, Brasil; dmlapola@unicamp.br, Telefone: +55 (19) 35212458

1. Introduction

Soils along the Amazon basin vary widely in geology and nutrient availability, which can affect forest productivity (Quesada et al. 2010, 2011, 2012). Nitrogen (N) and phosphorus (P) are two of the most essential macronutrients regulating plant growth and productivity in terrestrial ecosystems (Elser et al. 2007, Harpole et al. 2011). However, many other nutrients, such as potassium (K), calcium (Ca), iron (Fe) and zinc (Zn), also play important roles in plant metabolic processes and ecosystem functioning (Marschner 2012, León-Sánchez et al. 2019). Plants primarily obtain all these nutrients from the soil solution but in order to reduce their dependence on soil nutrient availability, plants have developed mechanisms to recover nutrients from senescing or old tissues and reallocate them to storage structures or production of newer tissues (Killingbeck 1996, Aerts and Chapin 1999, Brant and Chen 2015). While retranslocation can occur throughout the lifespan of the leaf (Ackerly and Bazzaz 1995, Wright and Westoby 2003), it is especially an intrinsic process of leaf senescence that occurs before leaf abscission (Aerts and Chapin 2000, Chapin et al. 2011).

Nutrient retranslocation capacity is measured as either retranslocation efficiency or retranslocation proficiency (Killingbeck 1996). Retranslocation efficiency (RE) is determined by comparing the nutrient concentration in senesced leaves with the nutrient concentrations in fully expanded, mature green leaves (Killingbeck 1996, Crous et al. 2019). Retranslocation proficiency (RP) measures terminal retranslocation ability of the leaf and represents the biochemical limit of retranslocation: more proficient leaves have lower senesced-leaf nutrient levels (Killingbeck 1996). The efficiency of nutrient retranslocation can be affected by many factors such as environmental conditions (Kobe et al. 2005, Vergutz et al. 2012), plant life-forms (Yuan et al. 2005, Jiang et al. 2012), growth stages (Yuan and Chen 2009b, Tully et al. 2013, Peng et al. 2016), leaf longevity (Wright and Westoby 2003, Achat et al. 2018) and canopy position (Tateno and Kawaguchi 2002, Yasumura et al. 2005).

Leaf nutrient concentrations and retranslocation play a major role in determining leaf-level nutrient-use efficiency (NUE) – the amount of dry matter production per unit nutrient taken up (Berendse and Aerts 1987, Killingbeck 1996, Aerts and Chapin 2000). In general, leaf nutrient concentrations can reflect the nature and strength of nutrient limitation in some ecosystems (Gusewell 2005) and the study of leaf nutrient concentrations and retranslocation in natural ecosystems can therefore indicate how individual plants cope with low nutrient availability and reveal feedbacks on nutrient cycling and plant productivity (Aerts and Chapin 2000).

Leaf longevity is a significant strategy used by plants to conserve nutrient and lessen dependency on soil pools (Chapin 1980, Aerts 1990, Escudero et al. 1992, Carrera et al. 2000). Longer lifespans support increased nutrient use efficiency (Chapin 1980, Chabot and Hicks 1982). Retranslocation can occur in other parts of the plant as well, such as roots before senescence and enables plants to store nutrients that will be redeployed in storage organs or new growth rather than lost with through tissue senescence (Chapin 1980).

However, factors other than nutrient concentration and longevity may also determine retranslocation efficiency. For example, plants growing at different solar irradiance levels can have widely different traits, since light availability varies within a forest vertical profile and more light is available to upper canopy than to lower canopy (Tateno and Kawaguchi 2002). The uppermost layer of a forest is occupied by canopy species, many of whose leaves will be in full sunlight, while the lowest layer is occupied by understory species that may be well adapted to shade (Hirose and Werger 1995). Knowledge of retranslocation patterns and their determinants is thus critical for understanding plant roles in ecosystem in different strata.

Globally, high proportions of leaf N (62.1%), P (64.9%), and K (70.1%) are resorbed before leaves are shed, while the ability of plants to resorb other nutrients is much lower (Vergutz et al. 2012). Retranslocation of essential elements like N, P, or K has received substantial attention in the literature (Kobe et al. 2005, Yuan and Chen 2009b, Freschet et al. 2010, Vergutz et al. 2012, Crous et al. 2019) whereas the retranslocation patterns of other elements, such as Ca, Mg, Zn, among others, have received much less attention (Wang et al. 2014, Achat et al. 2018). Due to its ecological importance for forest dynamics and maintenance, nutrient retranslocation data are also vital for the accuracy of ecosystem and biogeochemical models (Vergutz et al. 2012).

Nutrient retranslocation from plant tissues is a fundamental strategy for the conservation of nutrients in plants. However, the understanding of nutrient retranslocation processes in tropical trees is limited. Thus, in this work we investigated the effects of nutrient concentration in mature leaves, leaf longevity and canopy position to understand the process of nutrient retranslocation in trees in a mature lowland *terra firme* forest in Central Amazon, characterized by soils with low concentrations of P and cations. The specific objectives of this study were: (a) to determine the concentration of nutrients at different leaf ages; and (b) to estimate the retranslocation efficiency of nutrients at the community and ecosystem level and proficiency. In this work, the hypotheses were that the retranslocation is (1) influenced by the concentration of nutrient in the leaves; (2) influenced by leaf longevity; (3) influenced by the canopy position and alternatively (4) nutrient retranslocation does not vary in the studied community, due to the low availability of P soil.

2. Material and Methods

2.1. Study site description

This study was carried out in the experimental plots of the AmazonFACE Program (Free-Air CO_2 Enrichment) at the Experimental Station of Tropical Forestry (EEST/ ZF-2), maintained by the National Institute of Amazonian Research (Araújo et al. 2002). The station is located 60 km north of Manaus, Amazonas, Brazil. In the center of the selected two plots, there is one micrometeorological tower of approximately 40 m high, which allows access to the canopy of the twelve tree species studied. The trees studied include different species along the light profile, from small trees in the understory to canopy full sun crowns (adapted Dawkins 1963) (Table 1).

TABLE 1.Species, botanical family, species mean leaf longevity in days (±SD), total number of leaves used in the study, canopy position (UC = upper canopy, MC = middle canopy, US = understory) and crown height (m) of the twelve trees.

Species	**Family**	**Mean leaf longevity**	**No. leaves**	**Canopy position**	**Height(m)**
Diploon cuspidatum (Hoehne) Cronquist	Sapotaceae	265.27 ± 125.3	13	UC	28.6
Licania coriacea Sagot non Benth.	Chrysobalanaceae	327.20 ± 147.61	14	UC	26.8
Vantanea parviflora Lam.	Humiriaceae	367.37 ± 215.88	19	UC	26.8
Pteranda arborea	Malpighiaceae	537.54 ± 215.88	7	UC	26.8
Ocotea cernua (Nees) Mez.	Lauraceae	437.80±255.02	13	UC	23.2
Pourouma tomentosa Mart. ex Miq.	Urticaceae	196.56±84.94	16	UC	17.7
Pouteria caimito (Ruiz & Pav.)	Sapotaceae	733.53±188.86	20	MC	12.1
Mabea angularis Hollander	Euphorbiaceae	499.87±277.16	16	MC	14
Duguetia stelechantha (Diels)	Annonaceae	472.10±266.92	19	MC	14.1
Pouteria platyphylla (A.C.Sm.) Baehni.	Sapotaceae	432.00±238.28	18	US	6.6
Pouteria guianensis Aubl. & Eyma.	Sapotaceae	341.38±187.80	16	US	11
Erythroxyllum amplum Benth.	Erythroxylaceae	602.50±253.61	17	US	7.29

Notes: Total number of leaves used was of 188. Young= 70; mature=59 and senesced=59.

The region has a rainy tropical climate (Peel et al. 2007) according to the Köppen-Geiger classification, with mean monthly temperatures varying from 24 to 27 ºC and mean annual precipitation of 2400 mm, with a dry period between July to September, where monthly precipitation is less than 100 mm (Araújo et al. 2002, Peel et al. 2007). The average monthly irradiance above the canopies in the study area varies from 165 Wm^{-2} in the rainy season, to 230 Wm^{-2} in the dry season (da Rocha et al. 2009).

The soils are Ferralsols (oxisols), which are highly weathered (old) and well developed soils, deep, well drained, rich in clays (>70%), with low soil pH, low cation exchange capacity, high aluminum saturation, being rich in N (0.2% to 0.3%) and poor in total P (50 to 130 mg/kg), calcium, magnesium and potassium (sum of exchangeable bases ranges from 0.12 to 0.25 $cmol_c$/kg) (Quesada et al. 2011, Cordero et al. 2020). The vegetation is an old growth *terra firme* lowland forest (Araújo et al. 2002). The median canopy height is 30 m with emergent trees over 45 m tall (Vieira et al. 2004) and the average canopy cover is 87–89%, with a leaf area index of 5.3–6.2 m^2/m^2 and mean tree density (>10 cm DBH) of 708 individuals ha^{-1} (Pereira et al. 2019). The most representative botanical families of the studied site are Lecythidaceae, Sapotaceae, Burseraceae, Fabaceae, Chrysobalanaceae and Euphorbiaceae (Oliveira et al. 2008).

2.2. Leaf selection and longevity

Leaf-level demography has been monitored since 2016 by assessing the dynamics of leaf flush and shedding of leaves from selected branches (Menezes et al. under review). Leaf demography, and leaf age were tracked in 20 branches of each tree, depending on the access from the tower and total number of branches available (Table 1). The selected branches were marked with aluminum tags and monitored according to Reich et al. (2004) and adapted by G. Martins (personal communications, 2016). This approach consists of close monitoring of the stock, and the birth/death (i.e. leaf flush/abscission) dates of individual leaves for each census, also noting on the leaf position along the branch, whilst also acknowledging that the leaves already present on the selected branches had unknown flush dates (Menezes et al. under review).

Leaf longevity was measured using demography data, based on each species in the community, therefore young, mature and senesced categories were chosen according to their own longevity and classified individually and then categorized in each of the three classes used in the study. Here, we used young, mature and senesced leaf age categories, with the senesced category, containing the shed leaves that were tied to the branches by nylon strings to allow collection after leaf shedding (see details below). The canopy position of the trees was used as a proxy for light gradients of the forest vertical profile and trees were classified as: upper canopy, middle canopy and understory (Table 1).

For this study, green fully expanded mature and young leaves (i.e. known age) were previously collected and analyzed for element concentration. Also, senesced leaves from the same branches were collected using 0.30 mm nylon strings with one end tied at the base of the leaf limbus and the other to the branch where the leaf was attached. A total of 188 leaves were used (Table 1), the leaves were tied and numbered according to their position in the branch and the leaves (when senesced) were collected every fifteen days from August 2018 to December 2019.

2.3. Elemental analyses of plant material

After collection, leaves were dried for at least 48 h at 65 °C and then cleaned and milled to fine powder for chemical analyses. The concentrations of C, N, P, K, Fe, Zn, manganese (Mn), Ca and Mg were determined for each leaf. The contents of C and N were determined by a CN automatic analyzer (CN VARIO MAX, Elementar, Germany) as described in detail by Pella (1990). The other elements, except C and N were extracted using the nitric-perchloric digestion method (Miyazawa et al. 1999) and determined by the methods of ammonium molybdate spectrophotometry for P (Murphy and Riley 1965), and atomic absorption spectrophotometry for the other nutrients (Ca, Mg, K, Fe, Zn and Mn). The samples were analyzed at the Thematic Laboratory of Plants and Soils –INPA, Manaus, Amazonas.

2.4. Nutrient retranslocation calculations

Nutrient retranslocation was measured in two ways: retranslocation efficiency (RE in %) and retranslocation proficiency (RP in g kg^{-1}). The RE was calculated individually for all tree species and in the community level (average of all twelve tree species). RE is the proportion of nutrients retranslocated prior to leaf abscission and is measured as a function of the relationship between the senesced-leaf nutrient concentration (collected from the tied nylon string) and the mature-leaf concentration (Killingbeck 1996):

$$\text{Retranslocation efficiency} = \frac{([\text{mature leaf}]\text{DW} - [\text{senesced leaf}]\text{DW})}{[\text{mature leaf}]\text{DW}} * 100 \tag{1}$$

Where [mature]DW and [senesced]DW leaf represent a given nutrient concentration on a dry weight basis. RE derived from mass-based concentrations may underestimate the actual RE because they ignore changes in leaf mass during senescence (Aerts 1996, van Heerwaarden et al. 2003, Vergutz et al. 2012). However, Aerts (1996) suggested that this bias is likely to be small because leaf mass decline during senescence due to the withdrawal of soluble compounds is <10%. RE is a ratio, and thus indicates the amount of nutrients recycled by vegetation and may range from 0% to 90% (Chapin and Kedrowski 1983, Aerts 1996), but it may be driven by changes either in green or senesced leaves (occurring nutrient accumulation). Therefore, we also examined RP, assuming that RP was equal to senesced leaf (sl) nutrient concentration at the time of field sampling because leaves were collected when shed naturally (same samples used for RE). RP was measured by the final element concentration in the senesced leaves (sl) sensu Killingbeck (1996) as:

$$\text{Retranslocation proficiency} = [X]DW \text{ in sl} \qquad (2)$$

Where [X]DW is the concentration of a given nutrient in senesced leaves in a dry weight basis.

2.5. Ecosystem level nutrient retranslocation

To compare our community RE to the ecosystem level approach, we also calculated retranslocation efficiency from fresh canopy leaves and leaf litter collected in baskets (as commonly used for calculating litter productivity). We installed twenty-four 0.25 m^2 litter traps arranged around our towers in two plots (twelve per plot). Accumulated litter was collected every 15 days from January 2017 to December 2018. The biweekly samples were grouped into monthly samples for each collector. The samples were oven dried at 65 ºC until constant weight, and then cleaned to separate the main components: leaves, wood (diameter $\leq$ 2 cm) and reproductive material in the laboratory of the National Institute of Amazonian Research (INPA). Only leaves were used to determine nutrient concentration in litter. Nutrient concentration analyses and calculations follow the same methods as described in 2.3. and 2.4., respectively, but in this case were based on average concentrations for mature green leaves and average leaf litter concentrations from the mixed litter.

2.6. Statistical Analyses

We checked for normality of data with a Shapiro–Wilk test and used Levene's test to check the homogeneity of variance. Data on nutrient concentrations and nutrient retranslocation of young, mature and senesced leaves were not normally distributed, even after transformations. Thus, Kruskal-Wallis (kruskal.test function of the STATS package) non parametric test and Kruskal-Nemenyi post-hoc comparisons of means (posthoc.kruskal.nemenyi.test function of the PMCMR package, Pohlert 2014) were used to compare these variables among different leaf ages and canopy position. The correlation among nutrient concentration in mature leaves, leaf longevity and nutrient retranslocation were conducted by Spearman's rank correlation analyses. All statistical analyses were performed in R (R Core Team 2019, v. 3.6.0).

3. Results

3.1. Nutrient concentration throughout leaf age

Nutrient concentration changed in different leaf ages, with different patters found for different elements. Strongest decline in concentrations from young to senesced leaves was observed in P and K. As leaves aged, leaf P concentrations ranged from 0.64±0.22 to 0.28±0.12 g kg^{-1} and K from 8.27±2.33 to 2.90±1.99 g kg^{-1} ($p = 2.5e^{-14}$ and $p = 3.3e^{-14}$, respectively; Fig.1 c, f). Leaf N ($p = 0.0013$; Fig.1 b) showed a small difference in concentration between young and senesced leaves from 20.88±5.94 to 17.74±4.78 g kg^{-1}. Foliar concentrations of C (471.65±34.79 to 489.39±29.74 g kg^{-1}) varied between young and mature leaves, showing an increasing pattern, rather than a decrease ($p = 0.0082$; Fig.1 a).

Foliar concentrations for Ca ($p = 0.027$; Fig.1 d) showed a difference in concentration between young and senesced leaves from 2.99±2.79 to 4.43±3.78 g kg^{-1}, while Mg concentrations did not differ significantly among leaf ages. Leaf Zn showed a strong increase from young to senesced leaves varying from 28.13±11.76 g kg^{-1} to 65.18±39.57 g kg^{-1} and Mn from 55.71±38.62 to 79.69±53.35 g kg^{-1} ($p = 1.6e^{-11}$ and $p = 0.044$; Fig.1 i). For Fe, the difference was between mature and senesced leaves (216.81±151.68 to 328.78±228.19 g kg^{-1}, $p = 0.02$; Fig.1 g). In summary, senesced leaf nutrient concentrations of P, N and K were substantially lower than in younger leaves. In contrast, Ca, Fe, Mn and Zn concentrations were higher in senesced than in younger leaves, while C only varied from young to matures leaves and Mg did not varied at all.

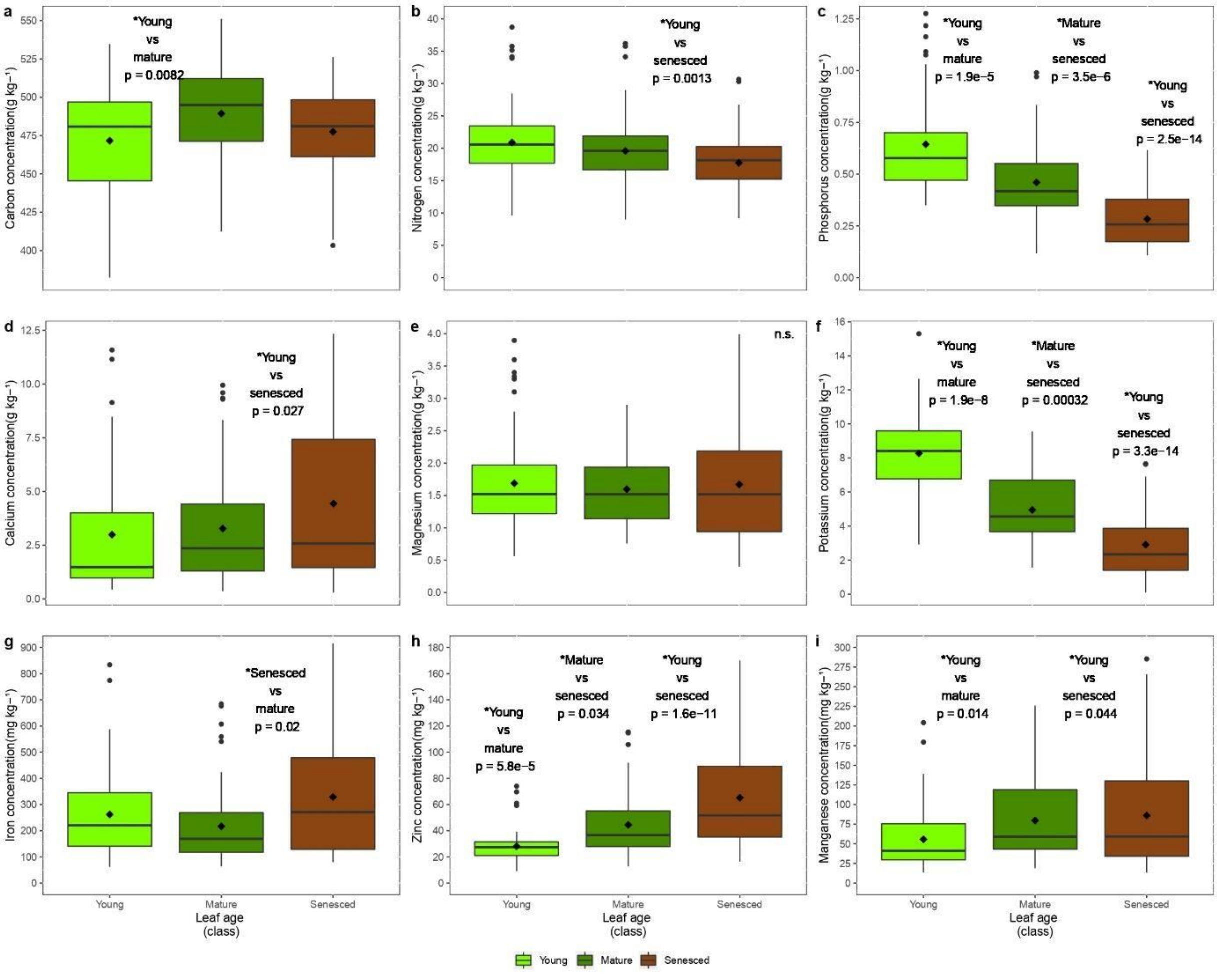

FIG. 1. Community level nutrient concentrations: (a) C, (b) N, (c) P, (d) Ca, (e) Mg, (f) K, (g) Fe, (h) Zn and (i) Mn. Leaf age categories are young (green; n=70), mature (dark green; n=59) and senesced (brown; n=59) leaves (see section 2.2 for definition). Boxplots represent mean community trees ($p < 0.05$, Kruskal-Wallis test; n.s., not significant).

3.2. Nutrient RE at community and ecosystem level and RP

The twelve tree species analyzed varied widely in their mean nutrient retranslocation efficiencies (Table 2). *L. coreacea* and *E. amplum* had the highest retranslocation for P (69.96±0.15% and 63.54±0.16%, respectively). For K, *P. guianensis* and *E. amplum* had the highest retranslocation (81.05±0.07% and 76.92±0.27%, respectively) in the community. *O. cernua* and *P. guianensis* were the species that most retranslocated N (26.85±0.09% and 18.80±0.12%). *P. caimito* and *M. angularis* accumulated (i.e. negative retranslocation efficiency) most Ca (-86.45±0.36% and -73.84±0.27%) than the other trees in the community. Zn was the micronutrient most accumulated, with *P. guianensis* and *M. angularis* accumulating more than a hundred percent of zinc (-183.98±0.56% and -140.25±0.79%). C was the least retranslocated among trees, with highest values for *P. guianensis* and *P. caimito* (8.47±0.04% and 6.32±0.05%).

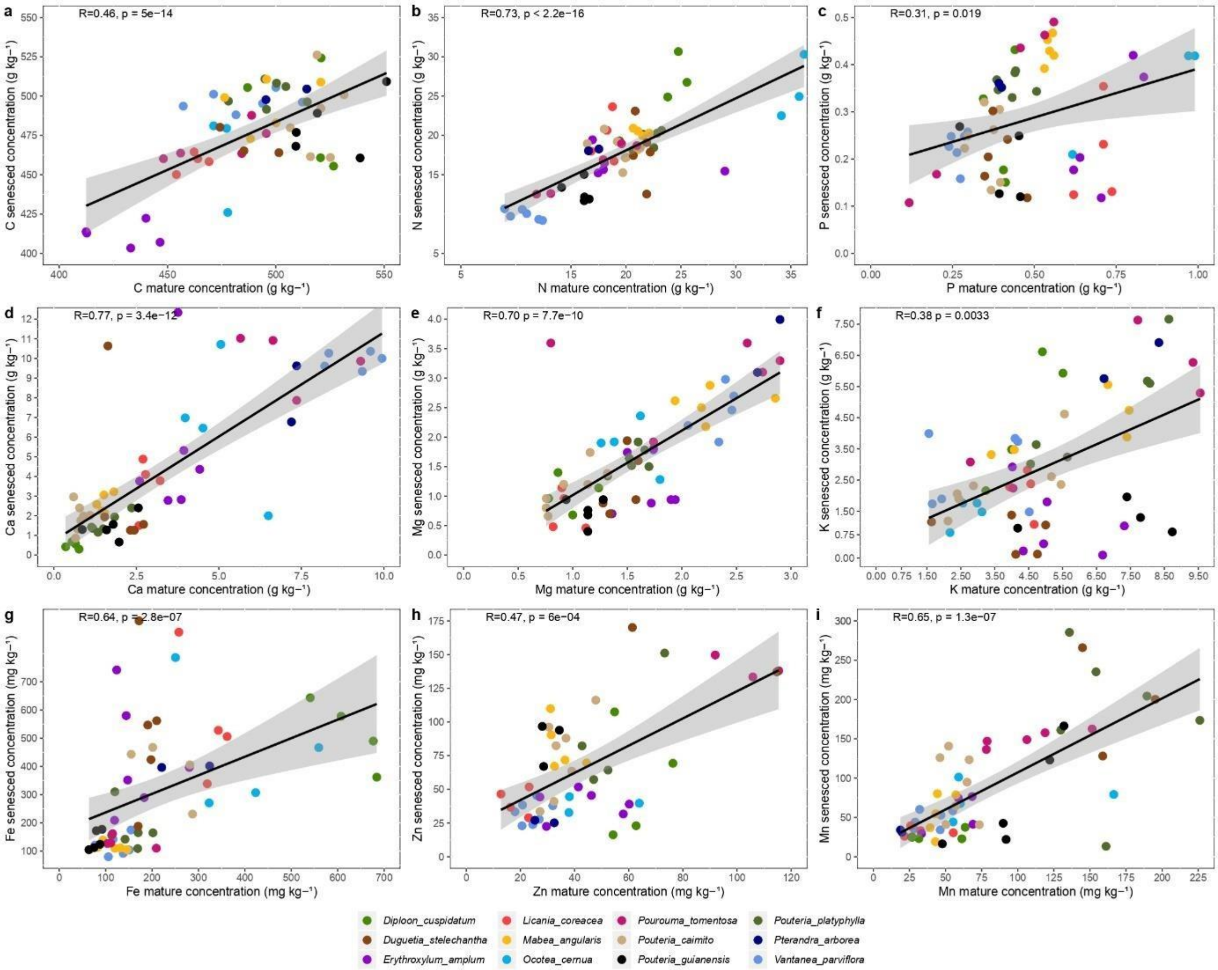

FIG. 2.Community level correlation between nutrient concentration in senesced leaves and nutrient concentration in mature leaves: (a) C, (b) N, (c) P, (d) Ca, (e) Mg, (f) K, (g) Fe, (h) Zn and (i) Mn (Spearman's rank correlation, p <0.05). Different colors indicate the twelve tree species analyzed in this study. Dashed red lines separate retranslocation and accumulation.

We observed strong mean nutrient RE (Table 2) and RP (Fig.1-brown boxplot; Fig.2) at community level. P and K were the nutrients most retranslocated in the community (33.24±0.20% and 42.03±0.23%, respectively), while N and C (Table 2) had the lowest retranslocation efficiency (6.89±0.11% and 2.67±0.03%, respectively). The macronutrient most accumulated in the community was Ca (-21.34±0.34%). The same accumulation occurred for all micronutrients, with Zn and Fe accumulating the most (-65.29±0.66% and -26.66±0.36%, respectively).

When comparing the average retranslocation from individual trees (community approach) and the retranslocation calculated from green leaves and litter from baskets (ecosystem approach), we observed that nutrient retranslocation was generally lower when using the community approach than for the ecosystem (Table 2). N, P, K, Ca, Fe, Zn and Mn all had lower estimates, while the opposite was observed for C and Mg (Table 2). Nevertheless, we found an overall similar pattern of nutrient RE in the ecosystem level (Table 2), but with P and K showing an almost two times higher RE (60.15% and 83.28%, respectively), N retranslocation in the ecosystem approach increased almost three-fold (22.7%), and C retranslocation (0.47%) decreased compared to the community. Ca and Mg accumulation show higher values in the ecosystem approach (-54.99% and -0.41%), and this trend also happened for Mn retranslocation (-58.02%). At last, the opposite trend occurred for Fe and Zn, which retranslocated (75.04% and 83.85%, respectively) in the ecosystem instead of showing an accumulation.

In terms of RP (i.e. concentrations in senesced leaves), we focused on N, P, K and C since these were the elements that showed retranslocation across community data Mean N proficiency in the community was low (17.74±4.78 g kg^{-1}) with most of the nutrient concentration remaining in the leaves after senescence (Fig.1 b). On the other hand, mean P proficiency in the community was high (0.28±0.12 g kg^{-1}), characterized by low nutrient concentration remaining in senesced leaves (Fig.1 c). Mean K proficiency was also high (2.90±1.99 g kg^{-1}), indicating that species with high retranslocation efficiency capacity are also more proficient (Fig.1 f). Finally, mean C proficiency was also low (473.18±32.26 g kg^{-1}) in the community.

TABLE 2. Species, number of leaf pairs and nutrients retranslocation. Means and ± standard deviations at community and ecosystem level.

Species	**CR (%)**	**NR (%)**	**PR (%)**	**CaR (%)**	**MgR (%)**	**KR (%)**	**FeR (%)**	**ZnR (%)**	**MnR (%)**
Diploon cuspidatum (4)	5.14±0.09	-11.81±0.10	31.66±0.33	9.04±0.38	-11.20±0.41	23.08±0.14	15.13±0.29	11.56±0.77	34.48±0.23
Licania coreacea (4)	0.88±0.01	-8.56±0.16	69.96±0.15	-25.94±0.52	17.34±0.40	50.88±0.18	-33.35±0.25	-134.45±0.98	-7.46±0.41
Vantanea parviflora (5)	-2.32±0.04	6.01±0.17	15.52±0.14	-12.37±0.10	-4.39±0.17	21.55±0.31	-0.57±0.36	-33.40±0.41	-26.44±0.39
Pterandra arborea (2)	0.72±0.02	-6.43±0.03	10±0.03	-12.45±0.26	-26.39±0.16	15.76±0.02	-51.67±0.39	7.83±0.21	-69.37±0.17
Ocotea cernua (4)	2.76±0.07	26.85±0.09	33.72±0.20	-40.23±0.78	-26.68±0.37	46.78±0.14	20.06±0.06	-10.18±0.49	-2.87±0.53
Pourouma tomentosa (5)	1.68±0.03	3.75±±0.06	11.12±0.04	-42.33±0.25	-18.87±0.13	30.79±0.21	-7.88±0.38	-36.13±0.23	-48.15±0.32
Pouteria caimito (7)	6.32±0.05	4.84±0.15	32.04±0.22	-86.45±0.36	-15.61±0.21	31.76±0.18	-81.34±0.30	-108.35±0.72	-16.49±0.52
Mabea angularis (5)	0.21±0.04	6.16±0.06	20.98±0.05	-73.84±0.27	-13.69±0.18	23.94±0.18	-6.35±0.34	-140.25±0.79	-16.67±0.51
Duguetia stelechantha(5)	5.11±0.02	15.95±0.19	46.55±0.20	27.65±0.36	18.27±0.30	73.58±0.28	0.25±0	-98.46±1.12	-22.23±0.54
Pouteria platyphylla (6)	-0.77±0.03	9.96±0.06	16.18±0.10	-3.81±0.15	-3.93±0.11	28.37±0.11	-23.30±0.71	-60.77±0.45	-13.25±0.68
Pouteria guianensis (5)	8.47±0.04	18.80±0.12	47.70±0.29	10.97±0.42	33.00±0.23	81.05±0.07	-72.58±0.31	-183.98±0.56	39.54±0.51
Erythroxylum amplum(6)	3.87±0.04	17.14±0.17	63.54±0.16	-6.34±0.32	30.00±0.31	76.92±0.27	-78.4±0.42	3.01±0.41	4.04±0.25
Community average	2.67±0.03	6.89±0.11	33.24±0.20	-21.34±0.34	-1.84±0.21	42.03±0.23	-26.66±0.36	-65.29±0.66	-12.07±0.30
Ecosystem average	0.47±0.01	22.70±0.25	60.15±0.60	-54.99±0.50	-0.41±0.01	83.28±0.77	75.04±0.80	83.85±0.90	-58.02±0.50

Notes: Leaf pairs are formed by mature and senesced leaves. Positive values are retranslocation and negative values are accumulation.

3.3. Effect of foliar nutrient concentration on retranslocation efficiency

Nutrient concentrations in the foliage were significantly and positively correlated to nutrient retranslocation efficiencies for all nutrients, except for K, Ca, Mg and Mn (Fig. 3). P mature leaf concentration varied from 0.11 to 0.99 g kg^{-1} ($p = 5.6e^{-05}$, $R=0.50$), with retranslocation varying from 1 to 80%. Other elements showed both RE and accumulation: C concentrations in leaves varied from 412 to 551 g kg^{-1} showing patterns of RE varying from 1.9 to 14%, but also, slight accumulation from 1 to -8% ($p = 0.001$, $R=0.44$). Leaf N concentration varied from 8 to 36 g kg^{-1} and also showed retranslocation varying from 0.5 to 46% and accumulation from -1.2 to -25% ($p = 0.049$, $R=0.26$). For micronutrients, Fe showed major accumulation within senesced leaves (Fig.3 f), with concentration varying from 63 to 684 mg kg^{-1}, showing retranslocation varying from 0.1 to 47% and accumulation ranging from -6 to -158% ($p = 0.002$, $R=0.33$). At last, Zn leaf concentration varied from 12 to 115 mg kg^{-1} also showing major accumulation from -3 to -263% and retranslocation from 1.5 to 70% ($p = 0.035$, $R=0.30$).

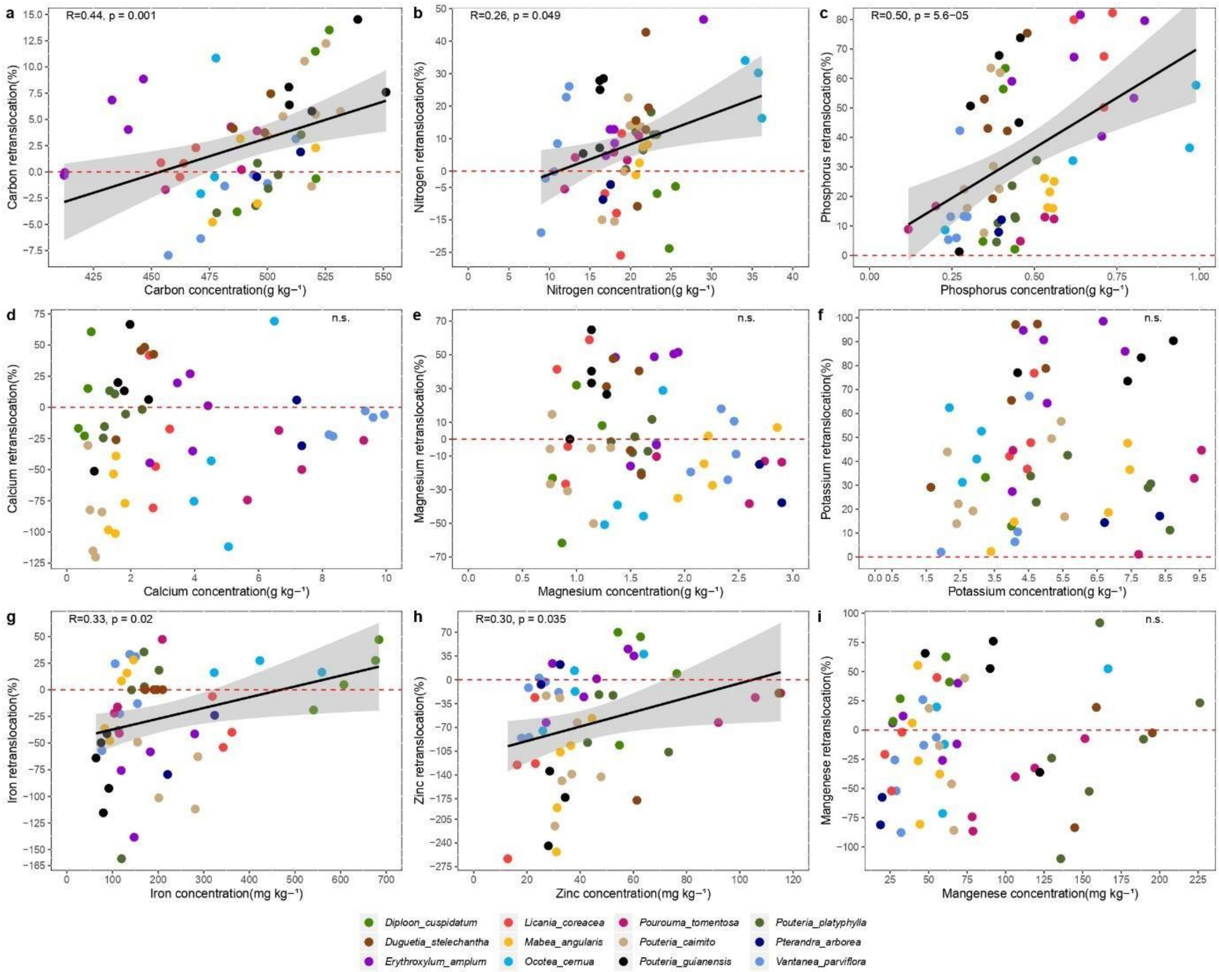

FIG. 3. Community level correlation between nutrient retranslocation efficiency (%) and nutrient concentration in mature leaves: (a) C, (b) N, (c) P, (d) Ca, (e) Mg, (f) K, (g) Fe, (h) Zn and (i) Mn (Spearman's rank correlation, $p<0.05$). Different colors indicate the twelve tree species analyzed in this study. Dashed red lines separate retranslocation and accumulation.

RE was negatively correlated to proficiency across the whole dataset, with exception of Fe (Fig. 4 g). Senesced leaf concentration (proficiency) had significant correlations with nutrient retranslocation efficiency for P and N and especially for K, Ca, Mg and Mn that were not significant when correlated with their nutrients on mature leaves. Even though the retranslocation and accumulation were similar for some nutrients, the effect was greater when retranslocation was correlated with proficiency. Thus, species with high retranslocation efficiency capacity are also more proficient.

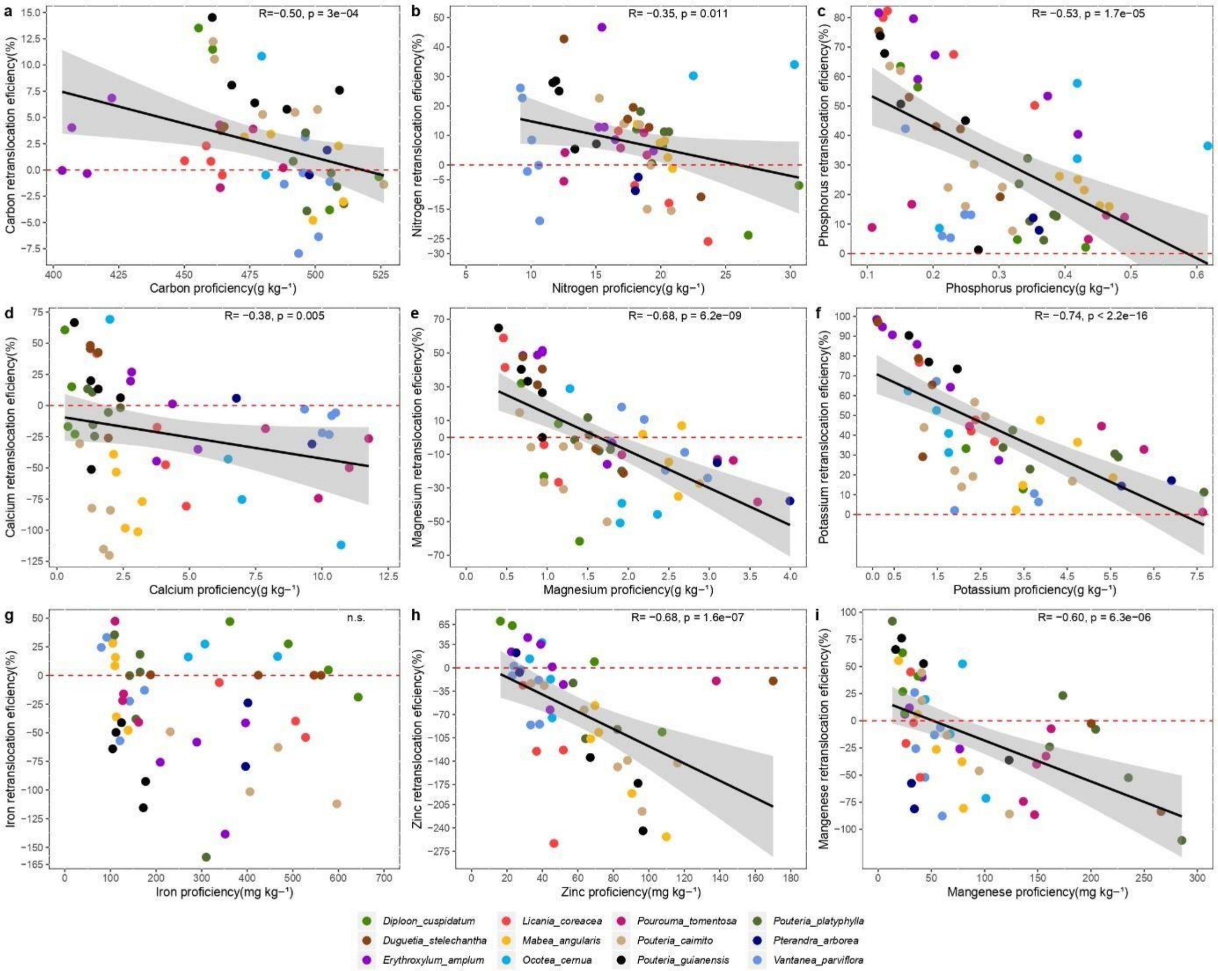

FIG. 4. Community level correlation between nutrient retranslocation efficiency (%) and nutrient proficiency: (a) C, (b) N, (c) P, (d) Ca, (e) Mg, (f) K, (g) Fe, (h) Zn and (i) Mn (Spearman’s rank correlation, p <0.05). Different colors indicate the twelve tree species analyzed in this study. Dashed red lines separate retranslocation and accumulation.

3.4. Effect of leaf longevity on nutrient retranslocation efficiency

Leaf longevity was significantly positively correlated with nutrient retranslocation efficiencies for the following elements: P, N, Mg, K and C (Fig.5 c, b, e and f). P retranslocation showed a strong correlation coefficient of R=0.43 (p = 0.00073) and higher retranslocation rate as leaf longevity increases. Following similar pattern, K showed an increase of retranslocation with increasing leaf longevity (p = 0.000021, R=0.49). For other nutrients, the accumulation during senescence resulted in different patterns from P and K. Although N retranslocation also showed a strong correlation coefficient (p = 0.00048, R=0.45) and a high retranslocation, this occurred somewhat simultaneously with mild accumulation. For C and Mg (p = 0.03, R=0.30;

p = 0.05, R=0.26, respectively) there was as much retranslocation as accumulation throughout leaf longevity.

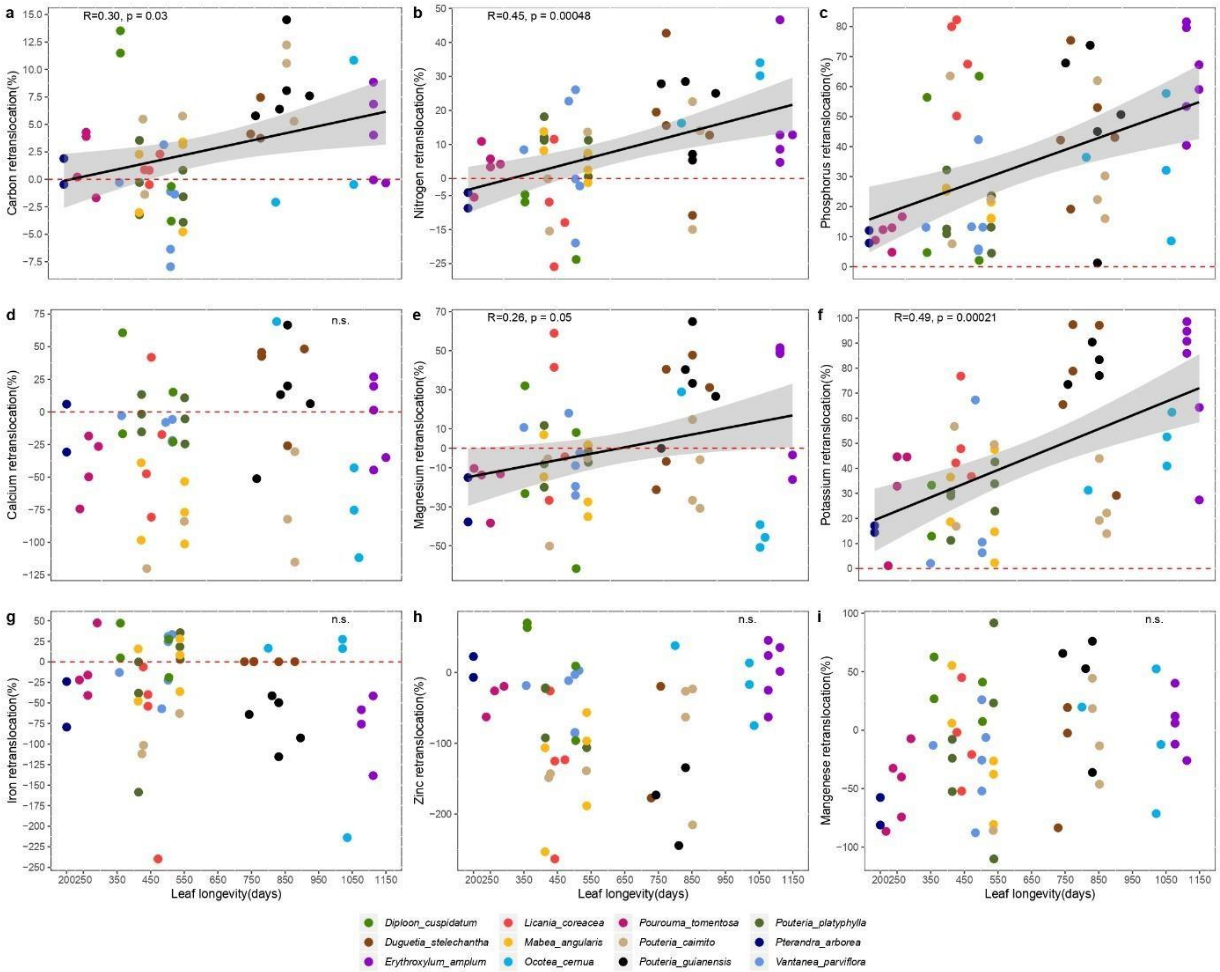

FIG. 5.Community level correlation between nutrient retranslocation (%) and leaf longevity (days) in an Amazonian rainforest: (a) C, (b) N, (c) P, (d) Ca, (e) Mg, (f) K, (g) Fe, (h) Zn and (i) Mn (Spearman’s rank correlation, $p < 0.05$). Different colors indicate the twelve tree species analyzed in this study. Dashed red lines separate retranslocation and accumulation.

3.5. Effect of canopy positions on nutrient retranslocation efficiency

Canopy position affected nutrient retranslocation only for tree elements: C, K and Zn (Fig.6 a, f and h). C retranslocation varied across positions, with lower retranslocation in leaves in upper canopy species (1.06±0.05%) than middle canopy (4.39±0.05%) species (p = 0.019; Fig.6 a). K retranslocation was significantly different between middle canopy (47±0.31%) and upper canopy species (24.78±0.27%), decreasing with canopy position (p = 0.056; Fig.6 f). While, Zn retranslocation also showed significant differences, with decreasing Zn retranslocation from middle canopy (-100.38±0.85%) to understory species (-18.75±0.47%) and from middle canopy (-100.38±0.85%) to upper canopy species (-33±0.70%) (p = 0.0022 and p= 0.0004, respectively; Fig.6 h), also decreasing Zn retranslocation, showing great level of accumulation of this micronutrient in different canopy positions. Overall, among understory, middle canopy and upper canopy, there were no significant differences for P, N, Ca, Mg, Fe and Mn retranslocation efficiencies (Fig. 6 c, b, d, e, g and i).

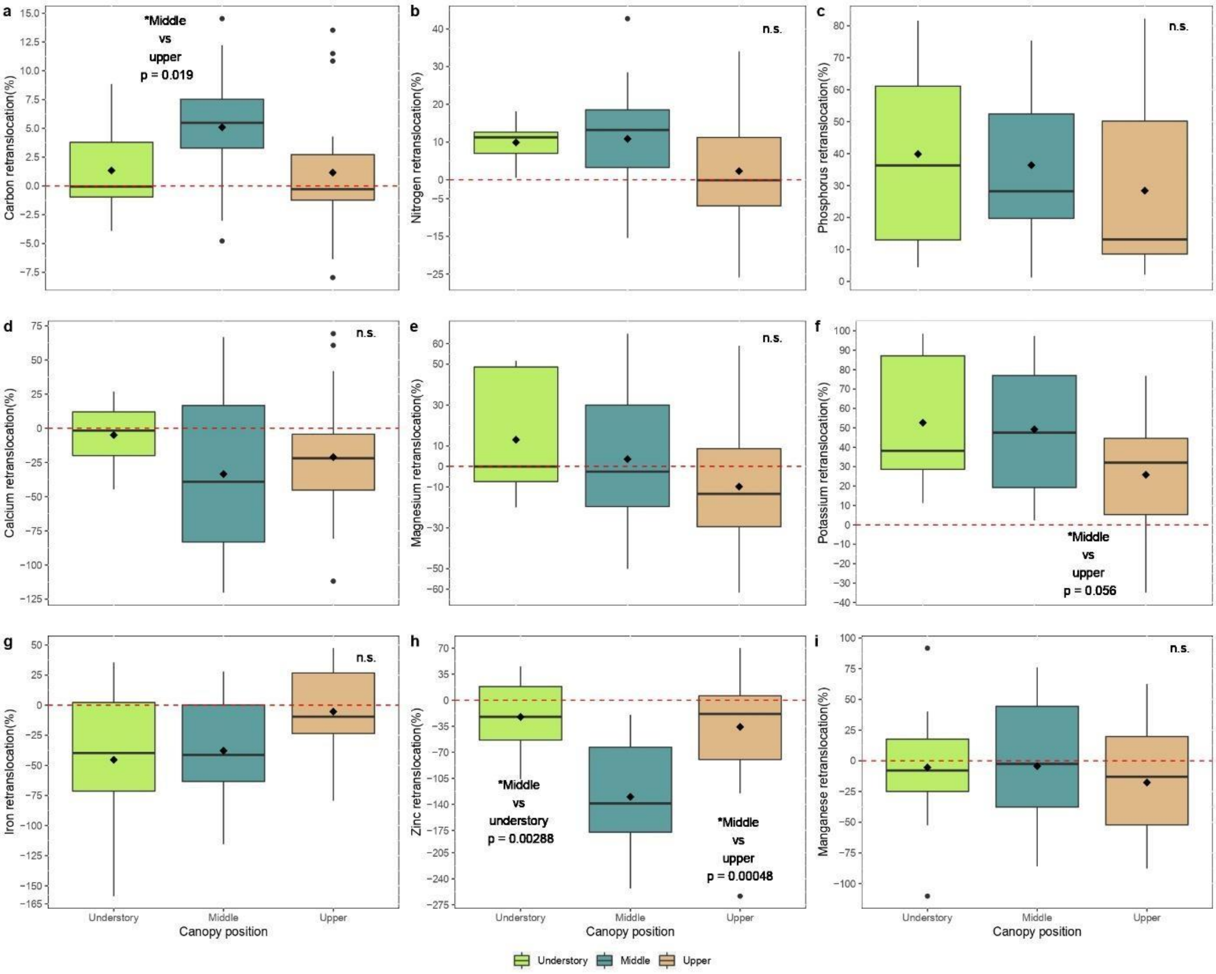

FIG. 6.Community level nutrient retranslocation: (a) C, (b) N, (c) P, (d) Ca, (e) Mg, (f) K, (g) Fe, (h) Zn and (i) Mn. Canopy positions are understory (light green; n=24 leaves), middle (blue; n=44 leaves) and upper (light pink; n=50 leaves). Boxplots represent mean community trees (p < 0.05, Kruskal-Wallis test; n.s., not significant). Dashed red lines separate retranslocation and accumulation.

4. Discussion

4.1. Leaf nutrient concentration across different leaf age classes influence in RE

The concentrations of N, P and K in leaves are flexible as plant grows (Richardson 2009, Alam et al. 2011, Amtmann and Rubio 2012), and leaf P, K and N concentrations (Fig.1) show lower values in senesced leaves (Huang et al. 2007, Vergutz et al. 2012, Yan et al. 2015). Such active nutrient mobility is related to its fundamental importance in plant metabolism. For instance, P is a central component of energy metabolism (ATP and Pi production) and is found in nucleic acids, lipid membranes and bioenergetic molecules such as ATP (Wright et al. 2004). Leaf P concentrations are often reported to decline with leaf age (Zhou et al. 2016, Achat et al. 2018, Prietro and Querejeta 2020) and this element is well known as being mobile in plants (Helmisaari 1992, Fife et al. 2008).

Leaf N concentrations were also previously reported to decline with leaf age (Koyama et al. 2008, Niinemets 2016, Albert et al. 2018, Wujeska-Klause et al. 2019) and this element is integral to the proteins of photosynthetic machinery, especially Rubisco (Field and Mooney 1986, Lambers et al. 1998) while also playing an essential role in the mobilization and storage of other key nutrients (Canton et al. 2005). Prior studies showed that leaf K also declined with age (Xue and Luo 2002, Zhou et al. 2016) and it plays a crucial role in stabilizing cell pH, regulating osmotic potential and carbohydrate translocation (Lansac et al. 1994, Marschner et al. 1997). Furthermore, K might influence N concentrations in leaves, photosynthetic activity and water use efficiency (Ericsson and Kähr 1993).

Due to leaf nutrient Ca (Fig.1) being non mobile inside plants there is low to no retranslocation linked with leaf ageing (McLaughlin and Wimmer 1999, White and Broadley 2003) also because of its association with structures, being a component of cell walls (Kumar et al. 2015). Consequently, and in agreement with previous studies (Liu et al. 2014, Yan et al. 2015, Prietro and Querejeta 2020), Ca concentration accumulated with increasing foliage age. Micronutrients, Fe, Mn and Zn showed similar tendencies with increased concentrations in senesced leaves (Prietro and Querejeta 2020), with Fe being involved in photosynthesis, mitochondrial respiration and N assimilation in plant tissues (Hänsch and Mendel 2009). Leaf micronutrients Mn and Zn showed higher values with leaf aging (Liu et al. 2014) and are involved in enzyme functioning and/or in regulation and can confer resistance against abiotic and biotic stresses to plants (Kirkby and Romheld 2004, Waraich et al. 2011).

The results presented here confirm what Killingbeck (2004) and Vergutz et al. (2012) previously found that the main nutrients withdrawn from senescent leaves are P and K, the macronutrients that are mobile, whereas Ca, is less mobile and is often accreted rather than resorbed at the end of the process. As for the younger leaves, our study showed higher concentrations for P, K and N when compared to the amount in the senesced leaves in the study, these nutrients are primary responsible to build up the carbon fixation and light harvesting machinery (Hikosaka 2005, Niinemets 2016). P concentration in younger leaves decreased about 32% as leaves aged (Crous et al. 2019). Leaf K was as well found to have higher concentrations in younger than in older leaves (Huber 1985). Leaf age also affects leaf N content, with larger N content in younger leaves than older leaves (Hikosaka et al. 1994, Niinemets, 2016). Thus, young and growing tissues generally contain higher concentrations of these nutrients (Mattson 1980, Harper 1989), because these tissues require more resources to support their rapid growth.

Even though correlations between RE and leaf nutrient status (mature leaf concentration) have not always been observed (Aerts and Chapin 2000, Hättenschwiler et al. 2008, Yuan and Chen 2009), an analyses of foliar nutrient concentrations in 92 global datasets (63% trees) (Kobe et al. 2005), indicated that N and P concentrations in senesced leaves were positively associated with concentrations of these elements in green leaves (Fig. 2) both among and within species. Therefore, resorption efficiency generally decreased with increased N and P in green-leaf status. That being the case, these results corroborated with our study, that also found similar results in our studied area, for both nutrients. RE reflects the trade-off of the energy cost for plants between taking up nutrients from soil and resorbing nutrients from senescent leaves (Wright and Westoby 2003, Jiang et al. 2012). It is also, expected to increase with decreasing nutrient concentrations in mature leaves, if taking up nutrients from soil with poor nutrient conditions is more difficult or expensive for plants than resorbing them from senescent leaves (Wright and Westoby 2003, Kobe et al. 2005, Kazakou et al. 2007). Also, concentrations of nutrients in senesced leaves influence ecosystem nutrient cycling by affecting litter quality and thus litter decomposition rates (Aerts and Chapin 2000, Kitayama et al. 2004, Wardle et al. 2009).

In contrast to our expectation, no correlation was found between K retranslocation and K concentrations in green leaves, similar result was found in a study of four emergent macrophytes species from nutrient-rich wetlands in Poland by Ławniczak (2011), suggesting possible leaching loss during senescence (Swift et al. 1979). Even though Ca retranslocation presented no correlation with Ca nutrient concentration, it was possible to see that some species retranslocated, instead of accumulating Ca. Hence, these results show that for some species Ca is not always retained in leaves and thus cannot reliably be used to obtain unbiased estimates of resorption efficiencies (Vergutz et al. 2012).

In the present study, Mg was not significantly correlated to their specific nutrient concentration in mature leaves. Consequently, this result is in agreement with a previous study by Achat et al. (2018), that found only low Mg retranslocation rates in deciduous tree species and none for evergreen species. Both micronutrients (Fe and Zn) were more accumulated than retranslocated in the community studied, this result is similar with the results from Liu et al. (2014) for twenty-two evergreen tree species in China. Although trace metals are sometimes resorbed, their active transport into senescing leaves may be in response to the need for functional catabolic enzymes (Killingbeck 1985). Overall, these results suggest that retranslocation may be an adaptive trait with considerable flexibility, even under similar soil conditions as the one in our study area.

4.2. Leaf longevity and nutrient retranslocation efficiency

As previously stated, leaf N, P and K concentrations show lower values in senesced leaves (Vergutz et al. 2012). At the community level, plant species with longer leaf longevity tend to have lower leaf nutrient concentrations (Aerts and Chapin 2000, Wright et al. 2004). During leaf senescence, these species are often assumed to have higher nutrient resorption efficiency than species with short life span to reduce nutrient loss (Aerts and Chapin 2000, Wang et al. 2014). In the present study, the same pattern occurred for the three essential nutrients. Consequently, species with long leaf life span are expected to have lower litter quality (high leaf litter toughness, C:N, lignin concentration) and decomposition rate (Huang et al. 2007). Wright and Westoby (2003) also found similar results, with positive correlations for N, P and leaf longevity in sites with high rainfall and low soil P. However, Reich et al. (1992) reported a significant negative relationship between the absolute amount of resorbed N and leaf longevity, although this negative relationship can sometimes not apply within species or among species at a site (Kikuzawa and Lechowicz 2011). While, Mg RE presented similar results found by Achat et al. (2018) for evergreen species on a global database study. The efficiency of retranslocation reflects plant physiology and metabolic processes (Wang et al. 2014). Therefore, increasing nutrient retranslocation and extending leaf longevity can be considered two determinants of nutrient conservation in plants (Escudero et al. 1992, Eckstein et al. 1999, Cordell et al. 2001).

4.3. Canopy position and nutrient retranslocation efficiency

Light availability largely varies with the canopy depth in a forest, since more light is available to upper canopy than to lower canopy trees (Tateno and Kawaguchi 2002). As a result, within a closed canopy, the availability of light can be reduced by up to 50-fold from the top of canopy compared with foliage in the shaded understory (Baldocchi et al. 2002). Such variations in irradiance can have marked effects on leaf morphological, chemical and physiological traits (Valladares et al. 2000, Meir et al. 2002, Kosugi et al. 2012). However, despite that, N and P RE did not vary among canopy position in the studied site. The same results were found for N retranslocation in a study of three deciduous woody species inhabiting a natural beech forest, where there were no significant differences among leaves under different growth irradiance of the forest (Yasumura et al. 2005). Thus, although retranslocation requires energy (Field 1983), energy per se does not seem to limit the extent of N retranslocation. Li et al. (2009) in a study in a southeastern Tibetan Plateau with evergreen and deciduous species found significant differences in P retranslocation in upper, middle and lower canopy species. Surprisingly, in our study P retranslocation was not affected by canopy position, what may be explained by Aerts (1996) in a meta-analysis with evergreen shrubs and trees which stated that although nutrient retranslocation is an important conservation mechanism at the species level, it does not differ strongly among growth forms, since the difference in retranslocation in these species is due to the nutrient concentrations in mature leaves prior to senescence. Besides, P leaf concentration was also not different among canopy position (data not shown) and similar results were found by Weerasinghe et al. (2014) studying canopy position effects in respiration and leaf traits in a tropical rainforest in Australia. Therefore, this can be evidence that the species in the community studied can optimize leaf anatomy and physiology to make the best use of the variable light encountered regarding of the its position on the forest vertical profile. Opposing results were found for C, K and Zn RE that were affected by canopy position. C and K presented higher RE values for middle canopy, than for upper canopy species and Zn accumulated less in understory species among all positions. Therefore, according to Demars and Boerner (1997) understory species, including shrubs, have lower retranslocation values than canopy species in the same area, this probably reflects the low light intensities common in forest understories.

4.4. Differences between nutrient RE in the community and ecosystem levels and RP

Most previous studies have focused on P and N retranslocation (Aerts et al. 1996, Kobe et al. 2005, Crous et al. 2019), overlooking other nutrients that are also important for nutrient cycling and ecosystem productivity (Vergutz et al. 2012, Reed et al. 2012, Liu et al. 2014, Prietro e Querejeta 2020). Mean nutrient RE estimates differed substantially among nutrients: RE was substantially lower in our community for N, P and K (see Table 2) than in the ecosystem, when compared to the global averages for evergreen species using newly fallen leaves, with a small subset of data collected from litter-trap studies (62.1%, 64.9% and 70.1%) for leaf N, P and K, respectively (Vergutz et al. 2012, Yuan and Chen 2009b). Despite of being lower than previously reported values, our results still indicate that retranslocation is an important nutrient conservation mechanism for these tropical species growing on highly weathered oxisols soils. K retranslocation is of particular interest, because it has received less attention in nutrient retranslocation studies (Kobe et al. 2005; Yuan and Chen 2015; Vergutz et al. 2012), although K constrains plant productivity in many ecosystems (Sardans and Peñuelas 2015).

Our data showed, on average, a modest C retranslocation efficiency in the community and ecosystem, with lower values (2.67% and 0.47%, respectively) than the global average of 23.2%, from Vergutz et al. (2012). This may be explained by the low variation in the C concentrations of mature and senesced leaves in the forest studied. Ca RE accumulated in both community and ecosystem (-21.34% and -54.99%, respectively), and as a structural element in plants, particularly in cell walls, Ca tends to be resorbed less during senescence than most other elements (Tukey 1970, Lambers et al 1998, Kazakou et al. 2007). Previous research has suggested that Ca is generally conserved in leaves (van Heerwaarden et al. 2003). Both community and ecosystem Mg accumulated (-1.84% and -0.41%, respectively) and showed different trend from the global averages of 28.6% estimated by Vergutz et al. (2012). Fe and Zn showed reversed trends in community and ecosystem (-26.66% and 75.04% for Fe) and (-65.29% and 83.85% for Zn). Both micronutrients have been showed to retranslocate, but also accumulate in previous studies (Killingbeck 1992, Killingbeck 1985). Recent studies suggested that multiple nutrients may co-regulate the carbon cycle, by affecting the functions and processes of ecosystems (Townsend et al. 2011). For example, many micronutrients shape litter production and decomposition rate (Kaspari et al. 2008). Mn enhances lignin degradation in the litter of many trees (Davey et al. 2007, Berg et al. 2010), while calcium (Ca) can affect tree growth and litter production (Paoli and Curran 2007) and forest floor litter turnover rate (Reich et al. 2005). Since litter quality (e.g. N, P and lignin concentrations) and quantity is the key factor controlling nutrient return to soils via litter decomposition (Freschet et al. 2012, Mao and Zeng 2012), changes in community structure and composition would exert a strong influence on ecosystem decomposition and nutrient cycling in this *terra firme* tropical forest.

The mean RP of N (17.74 ± 4.78 g kg^{-1}) and P (0.28 ± 0.12 g kg^{-1}) of the community plants were higher than the global averages of N (12.5 ± 0.3 g kg^{-1}; Yuan and Chen, 2009a) and lower than P (0.4 ± 0.0 g kg^{-1}; Yuan and Chen, 2009a); while mean value of K (2.90 ± 1.99 g kg^{-1}) was higher than the respective global averages (0.47 g kg^{-1}) reported by Liu et al. 2014. Mean RP of C (473.18 ± 32.26 g kg^{-1}) was also higher than the global average (430 ± 4.5 g kg^{-1}) reported by Yuan et al. 2009a. RP, defined as the level of nutrient concentrations in senesced leaves (Wright and Westoby 2003), was 0.28 ± 0.12 g kg^{-1} for P in the community studied. Killingbeck (1996) in a meta-analysis study of 77 deciduous and evergreen species, reported a biochemically complete retranslocation of P when the P concentration of senesced leaves in evergreen species is less than 0.4 g kg^{-1}, suggesting that leaves resorb all soluble P before senescence (Hidaka and Kitayama 2011); however, highly P limited systems may have senesced leaf concentrations as low as 0.01% (Hayes et al. 2014). The overall mean N concentration of 17.74 ± 4.78 g kg^{-1} in senesced leaves was higher when compared to the values of Killingbeck (1996) ($N<0.78$ g kg^{-1}) for evergreen species for complete retranslocation. This finding is consistent with results from a wet neotropical forest in Mexico that also demonstrated incomplete proficiency for the eleven plant species studied, with high nutrient concentrations in senesced leaves (Martínez-Sánchez 2003). Also, this high level of N in senesced leaves could be because the soils of the studied area have high concentrations of N, therefore, plants would not really invest in high RP here. Variation in nutrient resorption could also regulate stand-level biogeochemical cycling via its effect on litterfall quality, which, in turn, influences litter decomposition and soil nutrient availability (Aerts 1997, Yan et al. 2016).

4.5. Implications of low soil P in nutrient retranslocation

Our alternative hypothesis was that nutrient retranslocation of all nutrients could not vary in the community, due to the low availability of P in the soil. However, after analyzing our results, it was possible to confirm that there were variations found in the community retranslocation and they were more related to each nutrient and other process, despite the low availably of P in the soil, that ranged from 50 to 130 mg/kg (Cordeiro et al. 2020). Although nutrient retranslocation and the storage of large amounts of limiting nutrients in forests with high biomass may be a plausible mechanism to counterbalance the low availability of nutrients in the soil and to reduce the dependence on direct nutrient uptake (Grau et al. 2017), more studies should be made to try understanding other process above and belowground that can help explain how some species rely more in retranslocation than others and only for certain nutrients.

5. Conclusions

We concluded that in fact, foliar nutrient concentrations were different at different ages, and generally exhibited two trends, one was a higher trend for C, N, P and K and another was a lower trend for Ca, Fe, Zn and Mn. Nutrient concentrations in mature and senesced leaves influenced retranslocation efficiency, especially for P and K. There was no consistent pattern between retranslocation efficiencies and leaf longevity, but P and N declined with increasing leaf longevity. Canopy position was the least influential process in the retranslocation efficiency in the community. Furthermore, retranslocation efficiencies for P and K were higher than the N resorption efficiency both in the community and ecosystem levels. Taken together, these findings enhance our understanding of how these process impacts on nutrient cycling in this tropical forest, with the results having implications for vegetation–climate models that seek to predict nutrient influence of tropical ecosystems in future scenarios.

6. Conclusões

Concluímos que, de fato, as concentrações foliares de nutrientes foram diferentes em idades diferentes e geralmente exibiam duas tendências, uma tendência de queda para C, N, P e K e outra tendência de aumento para Ca, Fe, Zn e Mn. As concentrações de nutrientes nas folhas maduras e senescidas influenciaram a eficiência da retranslocação, especialmente para P e K. Não houve padrão consistente entre a eficiência da retranslocação e a longevidade das folhas, mas P e N declinaram com o aumento da longevidade foliar. A posição do dossel foi o processo menos influente na eficiência da retranslocação na comunidade. Além disso, as eficiências de retranslocação para P e K foram superiores à de N na comunidade e no ecossistema estudado. Coletivamente, essas descobertas aprimoram nossa compreensão de como esses processos afetam a ciclagem de nutrientes nessa floresta tropical, com os resultados tendo implicações nos modelos vegetação-clima que buscam prever a influência dos nutrientes em ecossistemas tropicais em cenários futuros.

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